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KASAHARA, HIROSHI. Japanese distant-water fisheries: A review 227
MATHER, FRANK J., III, ALBERT C. JONES, and GRANT L. BEARDSLEY, JR. Migration and distribution of white marlin and blue marlin in the Atlantic Ocean 283
GRAHAM, JOSEPH J. Retention of larval herring within the Sheepscot estuary of Maine 299
GRAHAM, JOSEPH J., STANLEY B. CHENOWETH, and CLARENCE W. DAVIS. Abundance, distribution, movements, and lengths of larval herring along the western coast of the Gulf of Maine 307
DAHLBERG, MICHAEL D. An ecological study of Georgia coastal fishes 323
HOAG, STEPHEN H. The relationship between the summer food of juvenile sockeye salmon, *Oncorhynchus nerka*, and the standing stock of zooplankton in Iliamna Lake, Alaska 355
VENRICK, E. L. Small-scale distributions of oceanic diatoms 363
LEIGHTON, DAVID L. Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success 373
SAILA, SAUL B., and JAMES D. PARRISH. Exploitation effects upon interspecific relationships in marine ecosystems 383
McCARTHY, JAMES J., and TERRY E. WHITLEDGE. Nitrogen excretion by anchovy (*Engraulis mordax* and *E. ringens*) and jack mackerel (*Trachurus symmetricus*) 395
JOHNSON, ALLYN G., FRED M. UTTER, and HAROLD O. HODGINS. Electrophoretic investigation of the family Scorpaenidae 403
VERNBERG, WINONA B., and JOHN VERNBERG. The synergistic effects of temperature, salinity, and mercury on survival and metabolism of the adult fiddler crab, *Uca pugilator* 415
JOHNSON, ALLYN G., and HOWARD F. HORTON. Length-weight relationship, food habits, parasites, and sex and age determination of the ratfish, *Hydrolagus colliei* (Lay and Bennett) 421
HENRY, KENNETH A. Ocean distribution, growth, and effects of the troll fishery on yield of fall chinook salmon from Columbia River hatcheries 431
HOOPES, DAVID T. Selection of spawning sites by sockeye salmon in small streams .. 447
BANSE, KARL. Redescription of some species of *Chone* Kröyer and *Euchone* Malmgren, and three new species (Sabellidae, Polychaeta). 459
BOOTH, DOUGLAS E. A model for optimal salmon management 497

Notes

ALVARINO, A. A second record of a rare siphonophore *Epibulia ritteriana* Haeckel 1888 507
DAVIES, ISAAC E., and ROBERT P. BRADLEY. Deep observations of anchovy and blue sharks from *Deepstar 4000* 510
ROTHSCHILD, B. J., and D. S. ROBSON. The use of concentration indices in fisheries 511
CARLSON, FRANK T., and JOHN W. REINTJES. Suitability of internal tags for Atlantic menhaden 514
GRAHAM, JOSEPH J. Filtration efficiencies of Boothbay depressor trawls 518

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Fishery Bulletin

CONTENTS

Vol. 70, No. 2 **April 1972**

KASAHARA, HIROSHI. Japanese distant-water fisheries: A review 227

MATHER, FRANK J., III, ALBERT C. JONES, and GRANT L. BEARDSLEY, JR. Migration and distribution of white marlin and blue marlin in the Atlantic Ocean 283

GRAHAM, JOSEPH J. Retention of larval herring within the Sheepscot estuary of Maine 299

GRAHAM, JOSEPH J., STANLEY B. CHENOWETH, and CLARENCE W. DAVIS. Abundance, distribution, movements, and lengths of larval herring along the western coast of the Gulf of Maine 307

DAHLBERG, MICHAEL D. An ecological study of Georgia coastal fishes 323

HOAG, STEPHEN H. The relationship between the summer food of juvenile sockeye salmon, *Oncorhynchus nerka*, and the standing stock of zooplankton in Iliamna Lake, Alaska 355

VENRICK, E. L. Small-scale distributions of oceanic diatoms 363

LEIGHTON, DAVID L. Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success 373

SAILA, SAUL B., and JAMES D. PARRISH. Exploitation effects upon interspecific relationships in marine ecosystems 383

McCARTHY, JAMES J., and TERRY E. WHITLEDGE. Nitrogen excretion by anchovy (*Engraulis mordax* and *E. ringens*) and jack mackerel (*Trachurus symmetricus*) 395

JOHNSON, ALLYN G., FRED M. UTTER, and HAROLD O. HODGINS. Electrophoretic investigation of the family Scorpaenidae 403

VERNBERG, WINONA B., and JOHN VERNBERG. The synergistic effects of temperature, salinity, and mercury on survival and metabolism of the adult fiddler crab, *Uca pugilator* 415

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HENRY, KENNETH A. Ocean distribution, growth, and effects of the troll fishery on yield of fall chinook salmon from Columbia River hatcheries 431

HOOPES, DAVID T. Selection of spawning sites by sockeye salmon in small streams .. 447

BANSE, KARL. Redescription of some species of *Chone* Kröyer and *Euchone* Malmgren, and three new species (Sabellidae, Polychaeta). 459

BOOTH, DOUGLAS E. A model for optimal salmon management 497

(*Contents continued on next page*)

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Notes

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CARLSON, FRANK T., and JOHN W. REINTJES. Suitability of internal tags for Atlantic menhaden 514
GRAHAM, JOSEPH J. Filtration efficiencies of Boothbay depressor trawls 518

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JAPANESE DISTANT-WATER FISHERIES: A REVIEW[1]

HIROSHI KASAHARA[2]

ABSTRACT

Most of the industrialized fisheries of Japan have developed under a licensing system controlled by the central government. Limitations on entry and the allocation of resources based on a variety of social and economic considerations have resulted in the development of an extremely diversified industry.

The postwar expansion of distant-water fisheries greatly accelerated the exploitation of resources in the North Pacific, as well as in many other areas of the world, and has caused numerous international conflicts. In addition to regional conventions for high seas fisheries, various bilateral agreements have been negotiated to cope with problems arising from jurisdictional claims by coastal states. While supporting narrow limits of national jurisdiction and the concept of free access to high seas fishing, Japan has accepted different forms of allocation as a means to accommodate the conflicting interests of the nations involved. Her domestic institutions and organization of the industry have helped the government make pragmatic arrangements with other nations. Whether or not a general agreement on fishery issues can be reached at the new Law of the Sea Conference, Japan will face more and harder international negotiations in view of the general trend of coastal states claiming broader zones of national jurisdiction.

Each of the main sectors of the Japanese fishing industry, including inshore fisheries, offshore fisheries, distant-water fisheries, and aquaculture, now operates under severe constraints. Although the total catch of distant-water fisheries is still increasing due largely to intensified pollack fishing in the Pacific, long-term prospects for further expansion do not appear bright. Little progress has been made in the utilization of abundant resources of unconventional species. Thus, the rapid growth of domestic fishery production is unlikely to continue. Increased joint ventures and other business arrangements in foreign countries may provide a partial solution. Import decontrol for fishery products would contribute substantially to meeting immediate problems of supply shortage.

This paper was originally drafted to provide, as part of the NORFISH study under the Washington Sea Grant Program which is supported by the National Oceanic and Atmospheric Administration, some background information on the development and the present status of the Japanese high seas fisheries, particularly those which have bearing on various international arrangements in the North Pacific. Since, however, discussions on the future regimes of the sea have been carried out with increasing intensity, the emphasis of the paper has shifted somewhat from descriptive information to a more analytical study of the international fishery problems faced by the Japanese government and industry, as well as the courses of action they are likely to take in response to future changes in international regulatory regimes. The importance of the topic in considering future international arrangements for fisheries is obvious, for the Japanese and Soviet distant-water fisheries have been among the major sources of international conflicts over fishery matters in various parts of the world. Although emphasis is on the North Pacific, developments in the rest of the world are also covered to the extent that they have bearing upon the situation in the North Pacific.

The present paper is not a comprehensive study of the Japanese fishing industry to examine closely all sectors of the industry, including inshore, coastal, and distant-water fisheries, as well as processing and marketing

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aspects. It emphasizes those fisheries the development of which have had substantial effects on international regulation of fisheries, except for such passing references to other elements of the industry as considered relevant.[3]

One of the serious problems about writing an English paper concerning Japanese fisheries is that fishery institutions in Japan are extremely complex and difficult to understand. It is almost impossible for foreigners to fully comprehend institutional aspects of the Japanese fishing industry without having been in the country for some time. English literature in this area is meager. Yet, domestic institutions for fisheries have had such tremendous effects on development of all Japanese fisheries, including those in distant waters, that it is often irrelevant to discuss their problems without having some understanding of the institutional framework in which they operate. To obtain some general information on this aspect, the readers of this paper are referred to four English papers: Oka, Watanabe, and Hasegawa (1962), Kasahara (1964), Comitini (1967), and Herrington (1971).

All high seas fisheries discussed in this paper are rigidly regulated by what is called "the licensing system." The system controls the activities of each fishery through restrictions on the total number of licenses to be issued, size of vessels to be used, area of fishing, method of fishing, and often species to be taken. Although the actual regulations under this system differ from fishery to fishery, a common, and most important, feature is direct control on the number and types of vessels to be used for a particular fishery. The justifications used by the government for imposing the limited entry system on offshore fisheries has varied. Among apparent objectives are: protection of inshore fisheries against offshore fishing, reduction of competition and prevention of disputes between different groups of offshore fishermen, stabilization of fishing conditions, maintenance of profitability, conservation of resources, prevention of international disputes, and others. Degree of success in achieving these objectives has also differed from case to case, but there is no question that the system has served as a powerful and convenient means to control each fishery and introduce such changes as considered desirable by the Japanese fishery administration.[4]

Practically all offshore and distant-water fisheries discussed in this paper are regulated by the central government. While legal authority is vested in the Minister of Agriculture and Forestry, the Fishery Agency (Suisancho), which is subordinate to the Ministry of Agriculture and Forestry, has in fact full power to control all major fisheries. There still exist a large number of small fisheries regulated by the provincial authorities, but they have practically no international implications, except those operating off the southernmost part of the Kurile chain and in Korean Straits. Chapter 3 of the Fishery Law, as amended in 1963, provides that anyone wishing to be engaged in any of so-called "designated fisheries" must be licensed by the Minister of Agriculture and Forestry, and spells out principles under which such licenses are issued. Administrative ordinances specify the designated fisheries and the types of regulation under which they operate. This category includes practically all important fisheries carried out in waters far from the home islands, as well as the coastal trawl fisheries conducted by medium vessels and purse-seine fisheries by medium and

[3] The author excluded whaling from the present paper due to lack of time. The history of the whaling industry is a story of its own, and may better be dealt with as a separate topic. Two nations, Japan and the Soviet Union, are more responsible than others for the present state of baleen whale stocks. Their recovery in the Antarctic would take many years even with restrictions more severe than those currently enforced. The relative importance of whaling in the Japanese fishing industry has decreased rapidly in recent years. While the omission of the topic affects the comprehensiveness of first two sections, its inclusion would not change greatly the substance of the last section.

[4] Scholars in North America approach the question of limited entry in fisheries mainly from the point of view of economic efficiency. Application of limited entry in the Japanese fishery administration is based on much more diversified considerations. The transferability of licenses, which is an essential condition for maintaining economic efficiency under this system, has been subject to increasing constraints in Japan. While the old fishery law established fishing rights as freely transferable private properties, the new fishery law (1949) specifically prohibited transfer. The new law also prohibited in principle the transfer of licenses for offshore fisheries; in reality licenses were still transferable in most cases; but the 1963 revision of the law further restricted the transferability of licenses.

large vessels. The only major fisheries which do not fall in this category are the saury and squid fisheries, which are regulated by separate ordinances.[5] Measures to further control the operation of the designated fisheries are provided in policies for licensing which are issued by the Ministry from time to time. Licensees of each of the designated fisheries are obliged to submit reports of their operation according to the format specified by the Minister.

In short, practically all important Japanese fisheries are strictly controlled by the central government under the licensing system. The administration of fisheries under this system is, of course, subject to pressures from different groups in the industry, including large fishing companies, vessel owner associations, and fishermen's associations, but changes in fishery policies are brought about only through this centrally controlled system. The system is also effective in accommodating such changes as the government and industry consider necessary for meeting new international developments. It is also responsible for the coexistence of many different types of fishing operation for catching the same species. For example, the present pattern of Japanese trawl fishing in the North Pacific, which employs all types of trawl gear and vessels of enormous size range, could not have developed without continuous manipulation of the system by the government under pressures from various sources.

REVIEW OF SELECTED HIGH SEAS FISHERIES

Most of the important Japanese fisheries are conducted on the high seas as defined by Japan. This review includes only those which have had or are likely to have international problems. Table 1 compares the catches (round weight) of such fisheries. Some of them, particularly trawl fishing by medium vessels and purse seining, are basically coastal, but they too have international implications in relation to the fisheries of Korea, China, and the Soviet Union.

[5] These fisheries are still not subject to strict limited entry, but saury vessels and larger squid boats must be approved by the Minister and thus are subject to various regulations established by the central government.

TABLE 1.—Catches of marine fisheries, 1969.

Categories	Catch	
	(Metric tons × 10^3)	
High seas salmon fisheries	123	
Tuna and skipjack fisheries[1]	586	
Trawl fisheries		
Distant water[2]	2,290	
China Seas	304	
Coastal	608	
Mothership crab fisheries	44	
Distant-water longline/gill-net fisheries[3]	27	
Large and medium vessel purse-seine fisheries	1,041	
Mackerel angling fishery	134	
Saury fishery	51	
Squid angling fishery	467	
All other fisheries[4]	2,301	
Aquaculture[5]	473	
Total	8,449	
Whaling	2,510	blue whale units
	6,668	sperm whales (head)
	627	small whales (head)

[1] Longline and pole-and-line (excluding catches by vessels smaller than 20 gross tons).
[2] Not including the China Seas.
[3] Other than tuna longline fisheries.
[4] Including inshore and coastal fisheries, as well as collection of clams (weight with shell) and seaweeds.
[5] Including oysters (with shell) and seaweeds.
Source: Ministry of Agriculture and Forestry (Japan) (1971).

TRAWL FISHERIES

Developments in the Prewar Period

A wide variety of fishing operations can be found even within one technical category, trawling. The coastal waters of Japan are crowded with a vast number of small draggers employing a great many different types of gear; over 800 Danish seiners and nearly 200 pair trawlers operate on the continental shelf and slope around and near the Japanese islands; a few otter trawlers and about 670 pair trawlers fish in the East China Sea (including the Yellow Sea); a fleet of motherships and factoryships, with trawl catchers of various types, is sent to the Bering Sea and the northeast Pacific, and a large number of independent trawlers to waters off Kamchatka and the northern Kuriles; many large stern trawlers operate in the Bering Sea and the northeast Pacific, as well as in West African waters; an increasing number of Japanese trawlers are found in the Atlantic waters off North America; and a few vessels trawl in waters off New Zealand and South Arabia. A brief review of historical sequences of development of trawl fisheries in Japan will help one understand how such a complicated pattern has emerged in this particular sector of the industry.

Different types of draggers for bottom fish have existed for several hundred years, and some of the primitive kinds can still be seen in inshore waters. The enactment of a law providing various incentives for development of offshore fisheries in 1898 and the introduction of two European-type trawlers (one imported from England and one constructed in Japan) in 1908 marked the beginning of modern trawl fishing in Japan. The fishery expanded very rapidly, the number of otter trawlers reaching 136 by 1912. This resulted in serious conflicts with inshore fishermen, prompting the government to issue trawl fishery regulations establishing large closed areas in coastal waters and to stop the application of subsidies to trawlers under the promotion law.

These measures forced otter trawlers to move into the East China Sea, leading to the discovery of new abundant resources of groundfishes, particularly highly valued porgies (sparids). The colonial administration of Korea immediately established large closed areas to shut out these trawlers from its coastal waters, thus pushing the fishery farther offshore. High costs of operation and overproduction, combined with a great demand for large vessels during World War I, resulted in a drastic reduction of trawl vessels, with only six remaining in 1918. The government, in 1917, established a new set of regulations and limited the total number of otter trawlers to 70, with a minimum size of 200 gross tons. This maximum number of 70 remained unchanged for many years for otter trawlers in the East China Sea (including the Yellow Sea).

Among the primitive methods of catching groundfishes, winddriven dragging and handhauling bottom fishing were considered most efficient in early years. With the introduction of powered vessels, the latter method developed into one somewhat similar to Danish seining. This fishery expanded very rapidly beginning in the 1910's and has since been a major source of conflicts between fishermen in inshore and coastal waters. The number of powered draggers exceeded 2,000 in the 1920's and became subject to new regulations in an attempt to control expansion and reduce conflicts with inshore fishermen. Meanwhile, the method of trawling by two vessels was introduced in 1920 and this fishery, too, began to expand at a rapid rate. Pair trawlers immediately started fishing in the East China Sea; the government then took action to control pair trawling in waters west of long 130°E under a separate set of regulations, the practice still in effect today.

Although both pair trawling and Danish seining became subject to ministerial regulations, the authority to issue licenses for these fisheries still lay in the prefectural governors. As a result, the expansion of the pair-trawl fishery in the China Sea continued, the number of its vessels reaching nearly 700 plus some 400 operating from the Japanese fishing bases in mainland China and Taiwan. In 1933, the authority to issue licenses for both pair trawling and Danish seining was transferred to the central government. The government then instituted a long-term plan to reduce these vessels, particularly Danish seiners in waters east of long 130°E, which were causing serious overfishing and conflicts with inshore fishermen. The plan was implemented for several years with some success, but with numerous problems arising from the increasing number of illegal vessels and violations of closed areas. The power to issue licenses (east of long 130°E) was transferred back to the provincial governments during World War II and remained there until 1947 when it was again given to the central government. A new cycle of various efforts to control the expansion of Danish seining and pair trawling and reduce the numbers of these vessels began in 1950-51, when the nation was still under occupation.

Regulatory measures taken during the prewar years to control the trawl fisheries of Japan established a pattern for allocating groundfish resources to different types of trawling: the stocks in coastal and nearby waters largely to the Danish-seine fishery (in the richest grounds off northern Honshu and Hokkaido) and partly to the pair-trawl fishery (in the western part of Japan); the stocks in the China Sea mainly to the pair-trawl and partly to the otter-trawl fishery; and the stocks in distant-water grounds to the otter-trawl fishery using large vessels.

Fishing in inshore waters was left largely to miscellaneous fisheries, including primitive draggers of various types. To a considerable degree, this pattern has persisted to the present, excepting some major changes in the allocation of fishing grounds in the northern North Pacific including west Kamchatka, the Bering Sea, and the Gulf of Alaska, as will be mentioned later. The coastal trawl fishery, mainly by Danish seines and partly by pair trawls, still remains the most difficult one from the point of view of fishery administration. Due to the long-established vested interests of different groups of vessels operating from different bases, the allocation of fishing grounds is extremely complex, as illustrated in Figure 1. In addition, there are closed areas around the home islands, some of which are rather extensive, different closed seasons applied in different areas, minimum depth limits in some places, as well as restrictions on the fishing bases each vessel can use for landing her catches.

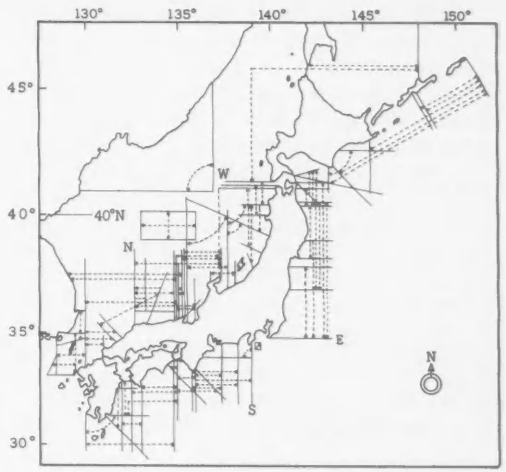

FIGURE 1.—Allocation of coastal trawl fishing grounds (from Norin Keizai Kenkyusho, 1965). Closed areas are not shown in the figure.

Post-World War II Developments

East China Sea trawl fishery.—Most of the otter trawlers and many of the pair trawlers were sunk by American submarines during the war, in most cases while serving as military transport vessels, and only eight otter trawlers were left when the war was over. To meet the serious shortage of food after the war, the government provided many incentives for reconstructing and expanding the fishing industry. The China Sea being the best trawl area in the nearby waters, the fisheries there recovered very quickly in spite of the so-called MacArthur Line limiting their fishing grounds to a narrow area of the continental shelf of the East China Sea. Numerous violations occurred and the area was later expanded slightly, but it was with the coming into force of the peace treaty in 1952 that the main fishing area became legally available to the Japanese trawl fishery.

By that time, however, 58 otter trawlers and 783 pair trawlers had been licensed, with the total fishing power far exceeding that of the prewar years. The catch per unit of effort, which had shown a remarkable recovery during the war time, started to decline sharply. Furthermore, due to international disputes with South Korea and mainland China, various restrictions were imposed on fishing operations. The expansion of the fisheries of mainland China (estimated to take roughly 70% of the total groundfish catch from the East China Sea, including the Yellow Sea) also affected the Japanese catch. Increased fishing for China Sea shrimp (*Penaeus orientalis*) improved the situation for a while, but the relative importance of the East China Sea grounds decreased rapidly as trawl fishing expanded into more distant areas, particularly the Bering Sea. Many of the otter-trawl licenses were used for obtaining new licenses for distant-water fishing by larger vessels, and there were only seven otter trawlers operating in the East China Sea by 1969. The number of pair trawlers also decreased, but to a much lesser extent. The use of pair trawlers as catchers of the Bering Sea mothership fishery also contributed toward reducing fishing pressure. Fishing in the South China Sea was also resumed in 1952 but ceased almost completely as the main fishing area, the Gulf of Tonkin, became unaccessible due to the Vietnam War.

It is important to know how the Japanese government encouraged the license holders of the trawl fisheries to move into distant waters. A policy for the otter-trawl fishery was established as early as 1950; those wishing to use otter trawlers currently licensed for fishing in the China Seas, or those proposing to abolish licenses for China Sea fishing in return for trawling in distant waters, were given priorities. A new policy on the replacement of distant-water trawl licenses (issued in 1967) is summarized in Table 2 as an interesting example of license conversion.

Coastal trawl fishery.—The trawl fisheries in coastal and inshore waters fall in two categories in the fishery administration of Japan: (1) inshore fisheries conducted by various primitive types of draggers of less than 15 gross tons each and (2) those by Danish seiners of over 15 gross tons and pair trawlers, pair trawlers being much less important except in the western part of Japan. What was referred to as the coastal trawl fishery in this section is the latter.[6] By the time the authority to license the coastal trawl fishery in waters east of long 130°E was again transferred to the central government, Japan was left with some 2,500 vessels plus a substantial number of illegal boats, and the number further increased to a maximum of over 2,800 in 1951, when a new plan for reducing them was instituted.

[6] The Japanese word for this category literally means "offshore powered trawl fishery."

TABLE 2.—Requirements for replacing a distant-water trawl vessel (in the North Pacific waters, including the Bering Sea, east of long 170°E, the Atlantic waters south of lat 40°N, and other distant areas) with a larger vessel.

Gross tonnage of existing license	Gross tonnage of new license	Licenses to be abolished
less than 550	up to 550	None
550-1,000	up to 1,000	None
over 1,000	over 1,000	None
less than 550	less than 1,000	(a) One or more distant-water trawlers, **or**
		(b) One or more Danish seiners (or pair trawlers) east of long 130°E with minimum aggregate tonnage of 50 RGT; **or**
		(c) One or more pair trawlers west of long 130°E; **or**
		(d) One or more large or medium purse seiners with minimum aggregate tonnage of 100 RGT; **or**
		(e) One or more distant-water tuna longliners with minimum aggregate tonnage of 300 RGT; **or**
		(f) One tuna mothership with three or more deck-loaded catchers.
less than 550	over 1,000	(a) Same as above; **or**
		(b) Two or more Danish seiners (or pair trawlers) east of long 130°E with minimum aggregate tonnage of 100 RGT; **or**
		(c) Same as above; **or**
		(d) Two or more large or medium purse seiners with minimum aggregate tonnage of 150 RGT; **or**
		(e) One or more distant-water tuna longliners with minimum aggregate tonnage of 600 RGT; **or**
		(f) One tuna mothership with three or more deck-loaded catchers.
550-1,000	over 1,000	(a) Same as above; **or**
		(b) One or more Danish seiners (or pair trawlers) east of long 130°E with minimum aggregate tonnage of 50 RGT; **or**
		(c) Same as above; **or**
		(d) One or more large or medium purse seiners with minimum aggregate tonnage of 50 RGT; **or**
		(e) One or more distant-water tuna longliners with minimum aggregate tonnage of 300 RGT; **or**
		(f) One tuna mothership with one or more deck-loaded catchers.

Source: Fishery Agency of Japan (1970).

Various measures were taken, including the combining of gross tonnages of smaller vessels to license a larger vessel, tighter control on illegal trawlers, compensations for giving up trawl fishing, and preferential licensing for transfer to other fisheries which were still in the process of expansion. During 1953-54, 285 licenses were transferred to other fisheries with compensations, a substantial number entering the tuna longline fishery. During 1954-56, when the salmon mothership fishery was still expanding rapidly, a large number of trawlers were converted into salmon catchers. Thus, a total of 910 licenses were taken out of the coast trawl fishery during 1953-56, with a total gross tonnage of 225,500 tons[7] (Norin Keizai Kenkyusho, 1965).

The most effective measure taken to reduce vessels operating in coastal waters, however, has been the expansion of trawl fishing grounds, which began in 1954. Danish trawling was expanded successfully into waters around the southern Kuriles, offshore banks in the Japan Sea, waters along Sakhalin and the Japan Sea coast of the Soviet Union, and, finally, waters around the northernmost part of the Kurile chain and both coasts of Kamchatka. Expansion into the northern Kuriles and Kamchatka waters marked a new era for Japanese land-based trawl fishing. By then, the Bering Sea trawl fishery, both by mothership fleets and large independent otter trawlers, was in full blast, and the mothership trawl fishery in waters off west Kamchatka had also started. A separate set of regulations, therefore, was established for fishing by trawl vessels licensed under the category of the coastal trawl fishery (see footnote 6). Great operational difficulties were encountered by the vessels engaged in fishing in these areas during the initial period, for they were largely from the existing fleet of coastal Danish seiners. Priorities for licensing were given to those having vested interests in waters around Hokkaido. Fishing area was originally defined as north of lat 48°N, east of long 148°E, and west of long 170°E, but was later expanded eastward to long 170°W with the western boundary moved to long 153°E. The fishery has grown very rapidly since 1963, and the present fleet consists of nearly 200 vessels (now called "Hokutensen," meaning vessels transferred to the north), most of them newly built stern trawlers (the upper limit of their size is set at 350 gross tons). The total catch of the fleet is nearly comparable to that of the entire mothership trawl fishery in the Bering Sea. The main fishing grounds are still in west Kamchatka and the northern Kuriles, but the amount of fish taken from east Kamchatka and the Bering Sea is also considerable. Out of the total catch of 768,000 metric tons in 1969, 670,000 tons were Pacific pollack (*Theragra chalcogramma*).

A second government plan to further reduce trawl fishing in coastal waters (the third in the history of Japanese fishery administration) started in 1962, again through the transfer of licenses to other fisheries. By that time, however, most of the other fisheries had reached or were reaching a point of saturation, and the effects of this plan were not too great. Some 30 licenses were transferred to the tuna and skipjack fisheries; a few licenses were issued for trawling in West Africa at the expense of those for coastal trawling.

Some remarks may be appropriate for the handling of the inshore trawl fishery. Emphasis of the fishery administration was on reducing the number of vessels through compensations and subsidies. Over 30,000 vessels existed in 1950, of which only 7,000 carried licenses issued by prefectural governments, the remainder being illegal vessels. The central government established policies and guidelines for the handling of this fishery, which included the definition of inshore draggers (called small bottom draggers) as vessels of less than 15 gross tons each; the establishment of nationwide limits on the total number, the combined gross tonnage, and the aggregate horsepower; the establishment of a target for reduction, etc. During the period 1956-61, a total of 2,342 vessels were scrapped to be used for "tsukiiso" (objects sunk in shallow waters to attract fish), 2,379 diverted to other

[7] The following numbers of trawl licenses were transferred to other fisheries, either converting vessels or giving up licenses in return for constructing new boats: 388 to the mothership salmon fishery as catchers, 102 to the tuna longline fishery, and 14 to the purse-seine fishery.

fisheries, and 75 converted to transport boats. But as of 1969, there still existed about 29,000 vessels, indicating that the reduction plan was not very successful. The fishery, however, is of relatively minor importance in the Japanese industry, its total production in 1969 being only 262,000 metric tons, roughly half of which consisted of shellfishes.

Mothership trawl fisheries in the Bering Sea and adjacent areas.—In the Japanese regulatory system, a mothership means a vessel with processing facilities aboard which is accompanied by one or more fishing vessels. Most of the motherships do not fish themselves, but large fishing vessels, such as factory stern trawlers, or large tuna longliners, are also defined as motherships if they are used for processing catches delivered by smaller fishing vessels. The trawl fisheries in the Bering Sea, Kamchatka, the Aleutians, and the Gulf of Alaska consist of three licensing categories: "the Northern Seas Mothership Trawl Fishery"; "the Northern Seas Trawl Fishery" conducted by independent trawlers; and "Hokutensen," mentioned above. Catches by these three categories in 1969 were 862,000 metric tons, 373,000 tons, and 768,000 tons respectively, the combined total being 2.0 million metric tons.

Trawl fishing in the Bering Sea was carried out even before and during World War II. As early as 1933, two fish meal factoryships with catchers were sent to Bristol Bay. The operation stopped after 1937 due largely to unprofitable fish meal trade. A freezer mothership operated in the Bering Sea in 1940 and 1941; a mothership operation for frozen and salted fish was conducted in waters off west Kamchatka during the war. The postwar mothership trawl fishery began in 1954 with two freezer motherships, accompanied by catcher boats, mostly otter trawlers, to produce frozen flounders, particularly yellowfin sole (*Limanda aspera*) in the Bristol Bay area. The number of freezer motherships increased to four in 1956, and a fish meal factoryship entered the fishery in 1958, as well as a mothership bottom-longline fleet. By 1961, the fishery expanded to include five fish meal factoryships (including one for processing *Atheresthes* for oil and meal) with 138 catchers, and 18 freezer motherships with 154 catchers. Three of the 18 motherships were specialized for shrimp fishing in an area near the Pribilof Islands, and eight (some of them were rather small) combined trawling, longlining (for halibut and sablefish), and gillnetting (for herring). The trawl catchers were from those licensed for fishing in the China Sea and coastal areas and included all three types: otter trawlers, Danish seiners, and pair trawlers. The Bering Sea trawl fisheries started as summer operations, but the season has since been extended, and some ships have been seen in the Bering Sea throughout the winter in the most recent years. For regulatory purposes, the Bering Sea was divided into several areas to allocate fishing grounds among different fleets taking into account their historical interests.

The next few years witnessed marked changes in the Bering Sea mothership trawl fishery. The yellowfin sole stock went down very quickly, as might have been expected for a hitherto unexploited flounder stock being subject to extremely intensive fishing, and also from past experience in waters along the Soviet coast (Kasahara, 1961). Thus, the operation of fish meal factoryships became unprofitable; this coincided with a slump in fish meal markets, both international and domestic. The number of factoryships manufacturing fish meal decreased from five (including one producing fish meal from *Atheresthes*) in 1961-62 to only two in 1963 (including one making a substantial amount of fish meal from *Atheresthes*), with the catch of flounders decreasing from 467,000 metric tons to less than 100,000 tons. A sharp decrease in the halibut catch, combined with a decline in the sablefish catch, made longlining less profitable. A sudden increase in herring production resulted in a market crisis. The shrimp fishery near the Pribilof Islands reached its peak in 1963 and declined rapidly thereafter. Meanwhile, emphasis has shifted from yellowfin sole to pollack, which is perhaps the most abundant species of commercial fish in the region. The introduction of a mechanized process to make minced pollack meat further boosted fishing for this species, and the catch has shown a phenomenal increase

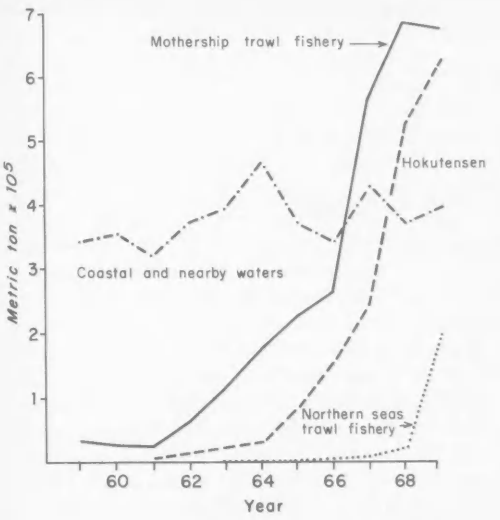

FIGURE 2.—Catches of pollack (*Theragra chalcogramma*) by Japanese fisheries, 1959-69 (from Ministry of Agriculture and Forestry, 1971).

(Figure 2). The number of vessels decreased to 12 motherships with 173 catchers by 1969, though with greater average tonnages of both motherships and catchers.

Trawl fishing in waters south of the Alaskan Peninsula began in 1960 when some of the catcher boats of a fish meal factoryship did exploratory fishing with trawls, longlines, and bottom gill nets. After 5 years of trial fishing, the government issued, in 1965, regular licenses for fishing in the Gulf of Alaska west of long 135°W under a different set of regulations. Exploratory fishing expanded into waters off British Columbia and the State of Washington. In 1967, the licensing of these vessels was combined with that of independent trawlers, mostly large stern trawlers, operating in the Bering Sea.

Independent trawlers in the northern areas.—Vessels in the category called "the Northern Seas Trawl Fishery" are licensed separately from vessels belonging to the mothership trawl fishery, but many of them are large stern trawlers sometimes accompanied by smaller trawlers (before 1967, some of these trawlers had been licensed as motherships). Emphasis is on ocean perch in the Gulf of Alaska and the Aleutians and on pollack in the Bering Sea. Distinction between this fishery and the mothership fishery is somewhat arbitrary, but it is reasonably correct to say that the former consists mainly of large stern trawlers, while the latter include motherships and factoryships accompanied by smaller trawl vessels of different types. In the Japanese regulatory system, the vessels of the former category have been licensed, since 1967, for fishing in both the Bering Sea and the Gulf of Alaska, while those of the latter category have been allowed to fish in the Bering Sea only.

Thus, the northern trawl fisheries have undergone rapid changes in the past 15 years. The exploitation of many of the important stocks has reached or exceeded the level of maximum sustainable yield, including yellowfin sole, halibut, sablefish, ocean perch, and shrimp (*Pandalus borealis*) in the Bering Sea; ocean perch in the Gulf of Alaska; and perhaps some others. Soviet fishing for flounders and ocean perch had additional effects on these stocks. The Japanese fisheries in Kamchatka and the Bering Sea are now largely dependent on one species, pollack, to be processed into fish meal and minced fish meat (on motherships and factory trawlers, as well as on land). The total amount of pollack taken in the Bering Sea and Kamchatka by the Japanese and Soviet fisheries now probably exceeds 2.5 million metric tons. Fishing intensity is still mounting, and effects of fishing are becoming apparent. The catch per unit of effort in the southeastern part of the Bering Sea has shown a decrease, and the average size and age of fish also have decreased. Fishing grounds have spread over the deeper portions of the central Bering Sea shelf. Further improvements in the method of catching pollack are under study, for pollack occur not only near the bottom of the shelf and upper slope but also in midlayers of deeper waters. The maximum level of exploitation will be reached fairly soon if it has not been already. There may be a further increase in the Japanese share of ocean perch in the Gulf of Alaska if Soviet efforts are drastically reduced. Japan has not fished for hake to any

extent, but the hake stocks have also been fished intensively by the Soviet Union. The potential of the herring stocks in the eastern Bering Sea, the cod stocks in the Bering Sea, and the sablefish stocks in southern areas are not well known, but it is not very likely that the catch of any of these species will substitute for a substantial portion of the present catch of pollack. As domestic markets for fish meal and minced fish meat remain strong, fishing pressure on pollack is bound to increase further.[8]

Certain actions by the Japanese government appear necessary in order to avoid a possible economic disaster: full assessment of the status of important stocks in the Bering Sea, Kamchatka, and the Gulf of Alaska; the establishment of catch quotas for pollack and a few other important species, in each of the three regions, in collaboration with the Soviety Union if feasible; and reallocation of fishing grounds among different sectors of the industry to make best use of the allowable catches. International problems arising from the development of trawl fisheries in the northern Pacific will be summarized in a later section.

Trawl fishery off west Africa.—The trawl fisheries in areas other than the northern North Pacific are licensed under the category "Far Seas Trawl Fisheries." The most important of these is the fishery along the west coast of Africa. The Soviet Union started trawl fishing off northwest Africa in the late 1950's and a few Japanese trawlers began fishing in 1959. In addition to local African vessels and Spanish and Portuguese boats, trawlers from a large number of non-African countries have fished in waters along the west coast of Africa. They include the Soviet Union, Japan, Poland, Italy, Israel, Greece, France, East and West Germany, Norway, Bulgaria, Romania, Belgium, South Korea, and China (Taiwan). The best trawl grounds occur in waters off northwest Africa and southwest Africa, more or less corresponding to the areas of strong coastal upwelling, that is, along Spanish Sahara and Mauritania in the north, and Angola, South-West Africa, and South Africa in the south. Trawl fishing in west Africa is very selective as to species caught, except in the south where hake predominate in the catches of most fleets. Japanese fishing has been mainly for cuttlefish (mongoika), octopus, and porgies (sparids) in the north; hake, porgies, and jack mackerel around the Cape; and mostly hake in waters off Angola and South-West Africa.

In the early years, the Japanese government was reluctant to increase the number of licenses for fishing in Africa. As it became obvious that other nations were intensifying their effort rapidly, the government relaxed its licensing policy and the number of vessels increased to about 70 in 1967, most of them large stern trawlers. The total catch in 1969 was roughly 240,000 metric tons. The Japanese fleet has been facing difficulty due to a decrease in the catch per unit of effort of high priced species and the expansion of national jurisdiction by the coastal states.

Vessels operating in the north are mostly based in Las Palmas, and Cape Town is the main fishing base for those in the southernmost area. Catches have been sorted out at these bases for transshipment to Japan or export to other nations. Ghana, Italy, Nigeria, Greece, and Romania have been among the main importers of trawl fish caught by Japan. Substantial amounts have also been landed directly in African ports for local sales—Lagos, Monrovia, Tema, Freetown, etc.

Trawl fishery in the North Atlantic.—Japan has made a substantial effort to develop a trawl fishery in the main international fishing area of the northwest Atlantic, particularly off Newfoundland, but the attempt has been an almost complete failure. She has, however, established a fishery in waters farther south, mainly off New York, as an attempt to divert seasonally some of the vessels operating in African waters. Some trawlers now plan to stay there almost year round. Main species are squid, butterfish, and argentine, with a total catch of 9,000 tons in 1969. Exploratory fishing has also been con-

[8] A 5,000-ton factory stern trawler has come into operation and several more in the same class are under construction, all to fish in the northern North Pacific. The Soviet Union has greatly increased fishing for pollack. South Korea has also begun pollack fishing in the northern areas.

TABLE 3.—Catches (metric tons × 10^3) of trawl fisheries in different categories, 1959-69.

Categories	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
Northern seas mothership trawl fishery[1]	169	472	639	534	338	438	404	454	778	844	862
Northern seas trawl fishery[2]	2	--	4	6	18	29	[3]62	[3]97	123	193	373
Hokutensen[4]	--	--	19	35	48	69	130	211	319	618	768
Atlantic and other seas	5	13	34	53	97	130	119	182	281	286	287
West of 130°E (China Seas)	357	368	375	331	345	302	325	334	338	326	303
Coastal trawl fisheries[5]	521	632	632	629	594	655	677	574	528	583	572
Inshore dragnet fisheries	239	230	213	215	208	209	230	253	269	276	259

[1] North Pacific and adjacent seas. Including small catches by gill net and longline.
[2] North Pacific and Bering, east of long 170°E.
[3] Including catches of the mothership fishery in the Gulf of Alaska.
[4] North of lat 48°N, east of long 153°N and west of long 170°W.
[5] East of long 130°E. "Offshore trawl fisheries" in Japanese terminology (see text).
Source: Ministry of Agriculture and Forestry (Japan) (1971).

ducted in waters off Florida. Although the New York fishery might expand further, it is unlikely to become a major trawl fishery comparable to that in Africa. Fishing in the North Pacific remains most attractive for large stern trawlers, and there are at present no plans to develop a major Japanese fishery in the main international fishing grounds of the northwest Atlantic.

Trawl fisheries in other areas.—Trawl fishing grounds in waters off New Zealand and Australia (west coast) were known to Japanese companies even before the war. Fishing after World War II started around 1959 largely for porgies (sparids). The trawl fishery off Australia has never developed to an important one, while trawling off New Zealand has expanded recently, the total catch in 1969 being 26,000 tons. Initially, the catch was mainly porgies (similar to Japanese "tai," *Chrysophrys*), but now barracouta (*Leionura*) is caught in large quantities, in addition to jack mackerel and porgies.

A Soviet fleet and some Greek trawlers fished in the Gulf of Aden along the South Arabian coast, before the closing of Suez, as well as in waters off northeastern Somalia. Soviet trawlers are fishing again along the Arabian coast. Japanese trawling in the Gulf of Aden began in 1966 for cuttlefish, porgies, and some other species; eight trawlers fished in 1967, with a total catch of 12,000 metric tons (Suisan-sha, 1970). This again has not developed to a major fishery.

Table 3 summarizes catches of the different trawl fisheries described in this section for the period 1959-69.

Mention should be made of the shrimp fisheries conducted by Japan in foreign countries after World War II (the Japanese did some shrimp trawling in Mexican waters during the prewar years). The oldest of these is the one along the northeast coast of South America. Shrimp fishing there has been developed mainly by American operators since about 1955. The establishment of a shrimp processing plant in Georgetown (Guyana, then British Guiana) marked the beginning of large-scale shrimping in that part of the world. Processing plants have since been built in Paramaribo, Cayenne, Port of Spain, Barbados, Belém, etc., and several hundreds of American shrimp boats are operating under various arrangements with the local governments and business groups. Shrimp grounds are generally between the Orinoco River mouth and the Amazon River mouth, with best areas located along the Guianas and northern Brazil.

Japan started shrimping in the region around 1959 and developed a small fishery based in Paramaribo. The Japanese government tightly controlled shrimping in that region for unknown reasons until 1967 when it relaxed restrictions. The total number of vessels licensed reached 72, including 50 land-based vessels and 22 vessels conducting mothership-type operations. Main bases are Georgetown, Paramaribo, and Port of Spain. Initially, shrimp trawlers built in Japan were used, but practically the entire fleet now consists of standard Gulf of Mexico shrimp trawlers constructed in the United States. The Japanese firms have formed a joint company apparently for the purpose of negotiating local arrangements.

Japan has also engaged in joint ventures for shrimp in India, Australia, Madagascar, Malaysia (Sarawak), and other countries. Recent

emphasis is heavily on shrimp ventures in Indonesian waters. After conducting exploratory fishing, several companies now plan to establish facilities at shore bases. The best grounds are along the north coast of Sumatra, the south coast of Borneo (Kalimantan), and the south coast of West Irian.

SALMON FISHERIES

Japanese salmon fishing from the Russian territory began in the latter half of the 19th century. After the Russo-Japanese War, the two governments entered into negotiations on the question of Japanese fishing rights along the Russian coasts. The resulting treaty of 1907 (went into force in 1908) greatly facilitated the expansion of Japanese fishing activities from the Russian territory. The treaty recognized the rights of the Japanese to fish along the Russian coasts of the Japan Sea, the Okhotsk Sea, and the Bering Sea, including the entire coastline of Kamchatka, the most important salmon-producing area in Asia. A large number of lots for salmon trap fishing were distributed, by auction, between the Russians and Japanese (Leonard, 1944; Kasahara, 1961).

After the Russian Revolution, a temporary arrangement was made until a new treaty was signed in 1928 after long negotiations. The new agreement modified the arrangements of the 1907 treaty, but the rights of the Japanese to fish from the Russian territory were reestablished. The Soviet government thereafter tried to expand the fishing activities of its nationals by reducing the proportion of lots leased to the Japanese, resulting in continuous controversies and negotiations. The amount of Japanese fishing for salmon in the Soviet territory was reduced drastically after 1941, when the Pacific War broke out, and the entire fishery came to an end in 1944.

While negotiations for the allocation of fishing lots were going on between the two governments, the Japanese began to engage in a mothership-type salmon fishery in waters off Kamchatka (motherships were anchored outside the territorial sea). The fishery lasted from 1929 to 1942. More important was the development, during the 1930's, of drift net and trap fishing based in the northernmost islands of the Kurile chain,[9] which intercepted a large number of salmon on their way to the streams in the Kamchatka Peninsula and other areas of Russia. (See Kasahara, 1963, for catch statistics.) It appears peculiar that such new developments, which no doubt had substantial effects on inshore salmon catches, did not result in a serious controversy during the prewar period. If these offshore fisheries had continued, difficult problems would have developed not only between Japan and the Soviet Union but also between different Japanese fisheries catching salmon. In any case, these developments clearly indicated what the Japanese might do if they were excluded from fishing salmon in inshore waters.

Article 9 of the San Francisco peace treaty states, "Japan will enter promptly into negotiations with the Allied Powers so desiring for the conclusion of bilateral and multilateral agreements providing for the regulation or limitation of fishing and the conservation and development of fisheries on the high seas." The North Pacific fishery treaty was signed on May 9, 1952, immediately after the peace treaty entered into force on April 28 of the same year.

Expecting the abolishment of the so-called MacArthur Line restricting Japanese fishing grounds during the occupation period, the Japanese government issued, early in 1952, its policies on the resumption of the high seas salmon fishery. Three motherships with 50 catchers and 12 scouting boats were licensed. Each of the three biggest fishing companies, Taiyo, Nippon Suisan, and Nichiro, was authorized to operate one mothership, with Danish seiners from the coastal trawl fishery east of long 130°E (mentioned previously) employed as catcher boats. The fleet left Japan just 3 days after the peace treaty came into force. Although the North Pacific treaty had not been ratified by Canada, fishing was authorized only in waters west of long 175°W and between lat 48°N and 55°N; waters off Kamchatka and the northern Kuriles were avoided. The fishery differed entirely from

[9] The entire Kurile Islands and the southern half of Sakhalin belonged to Japan until the end of World War II.

the mothership fishery before World War II, which was conducted in waters very close to the Kamchatka Peninsula. The result was a smashing success, and this set a pattern for further development of the mothership salmon fishery on the high seas. The land-based drift-net fishery, too, operated in a large area of the high seas; 1,500 drift netters fished for salmon, mostly pink salmon heading for Soviet streams. The government issued new regulations for the land-based drift-net fishery.

By 1955, the mothership expanded to 14 motherships, including 2 in the Okhotsk Sea, with 344 catchers and 58 scouting boats; the land-based drift-net fishery was conducted by 325 larger vessels (over 30 gross tons) licensed by the central government and more than 1,200 smaller vessels licensed by the prefectural governments. The mothership fishery took 64 million salmon (in number of fish) and the land-based fishery 47,000 metric tons (in round weight). Japan had planned to increase the number of motherships to 19 in 1956 with a corresponding increase in the number of catcher boats.

In February 1956, the Soviet Union took unilateral action to restrict high seas salmon fishing in the northwest Pacific (west of long 170°E). The two governments entered into negotiations for a fishery treaty, which was concluded on May 15 and entered into force a few months later. The diplomatic relations between the two nations were restored later in the year. The new fishery treaty set forth a wide variety of regulations, including large closed areas, closed seasons, catch quotas, restrictions on fishing gear, and arrangements for enforcement (a system of inspection by the Soviet authorities). Many changes have taken place since then, including the development of a large longline salmon fishery on the high seas and a substantial salmon fishery in the Japan Sea, expansion of the regulatory area, changes in the allocation of fishing grounds and catches between different Japanese fisheries, the closure of the entire Okhotsk Sea, and continuous modifications of the domestic regulations to meet the international situation. The pattern of salmon fishing as of 1969 is summarized in Figure 3. The number of catchers has been reduced substantially by transferring their licenses to the tuna longline fishery and the northern trawl fishery. Due to expansion of the regulatory area and a continuous reduction of the catch quota under the treaty, which was considered necessary by the Soviet Union for conservation, the total take of salmon by Japan (including small amounts of salmon destined for Japanese streams) decreased from 197,000 metric tons in 1958 to 141,000 metric tons in 1969 (Ministry of Agriculture and Forestry, 1971).

In short, the expansion of the Japanese high seas salmon fisheries came to an end already in the 1950's when regulatory measures under the Japan-Soviet fishery treaty were applied to practically all areas of the northwest Pacific in which salmon were found. Offshore fishing must have had adverse effects on the salmon stocks in general, but the exact nature and extent of such effects are not well understood from the data and information exchanged through the Japan-Soviet fisheries commission.

The eastern boundary of the offshore salmon fishing grounds was established at long 175°W under the North Pacific treaty. In spite of extensive research conducted on the offshore distribution of salmon, resulting in a wealth of scientific information, and continuous hard negotiations between the national sections of the North Pacific fisheries commission, this provisional line has remained unchanged to date. Substantial quantities of Bristol Bay sockeye salmon have been taken by the Japanese mothership fishery in years of large runs, but none of the three parties has seriously considered the termination of the treaty, which could have been done at any time after 1963 with 1 year's advance notice. Thus, the provisional line drawn in 1952 has proved to be a good political compromise as far as these three countries are concerned.

CRAB FISHERIES

Three species of king crab (*Paralithodes*) and tanner crab (*Chionoecetes* spp.) have been exploited by the high seas crab fisheries in the northern North Pacific. The most important are the true king crab (*P. camtschatica*) and the tanner crab. Abundant resources occur in

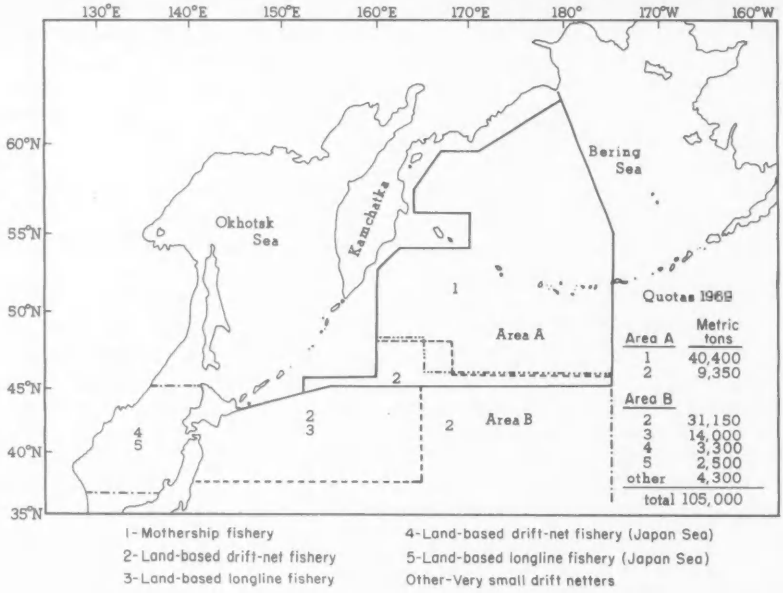

FIGURE 3.—Allocation of high seas salmon fishing grounds, 1969 (from Suisan-sha, 1970).

waters off northern Japan and Sakhalin, Kamchatka (particularly the west coast), the eastern Bering Sea, and the east Aleutian-Kodiak area. Land-based crab fishing for manufacturing canned crab dates from 1905; it expanded from Hokkaido to Sakhalin and the northern Kuriles. Exploratory attempts for fishing with motherships began in the 1910's along the west coast of Kamchatka, and commercial fishing of this type started in 1921. Stimulated by growing international markets for canned crab, the fishery expanded rapidly and the government, as usual, issued king crab mothership fishery regulations in 1923. The number of motherships was limited to 18 in 1927. Attempts were also made to develop crab resources along the east coast of Kamchatka without much success. The mothership crab fishery in Bristol Bay began in 1930 and continued until 1939 (no fishing in 1931). It never developed to a major fishery before World War II, only one mothership operating in most years. Crab fishing from the Russian territory was first conducted in connection with salmon fishing, but it was in 1920 that an official arrangement was made between the Russian and Japanese governments to permit Japanese crab fishing from the Russian territory (west coast of Kamchatka) under Russian regulations. (The Japanese salmon and crab fisheries from the Russian territory were practically monopolized by one company, Nichiro.) Both mothership crab fishing and land-based fishing employed tangle nets; motherships carried small powered boats called "kawasaki-sen" to do the fishing and were equipped with canning lines to process crabs aboard.

As in the case of the salmon mothership fishery, the Japanese government issued its policies on the resumption of the Bristol Bay crab mothership fishery prior to the entering into force of the peace treaty in 1952. Because of political repercussions from the United States, no fishing was authorized in that year, and only one mothership was licensed for 1953 as a joint operation by the three biggest fishing companies, Taiyo, Nippon Suisan, and Nichiro. Specific regulations were issued to limit the number of deck-loaded boats as well as self-navigating fishing

vessels (for scouting and setting nets), the amount of canned crab produced, and the amount of tangle nets used. This form of operation continued until 1959 without a major expansion, except for a substantial increase in the production quota in 1959. A second mothership fleet was authorized to operate in the Bering Sea in 1960 to produce frozen crab. The fishery thereafter grew very rapidly until 1964, when a record catch of over 10 million crab was made.

Having declared exclusive rights to exploit king crab resources under the 1958 continental shelf convention (entered into force in 1964), the United States initiated, in 1964, negotiations with Japan concerning the crab fishery in the eastern Bering Sea. Since then, the Japanese catch has been reduced continuously under international agreements between the two governments.

The first Soviet mothership crab fleet entered the eastern Bering Sea in 1960, resulting in direct competition with the Japanese fishery. The U.S. crab fishery in the Bering Sea remained of minor importance through 1963, with no fishing conducted in some years. U.S. vessels from Kodiak and adjacent areas moved into the Bering Sea in 1964 and their catch has been increasing since then. Traditionally, Japanese fishing was by tangle nets and U.S. fishing in waters south of the Peninsula was by pots (some U.S. vessels used to trawl for crab in the Bering Sea). Now pot fishing is conducted both by the Japanese and the Americans, complicating the situation further. The Japanese and the Soviets have also developed a system of allocating tangle-net fishing grounds between their fleets. As the eastern Bering Sea king crab stock began to show signs of depletion, Japan intensified fishing for tanner crab, which is also very abundant in the eastern Bering Sea. Tanner crab fishing is now as important as king crab fishing and, through a quota, under control by the Japan-United States agreement.

The Japanese mothership crab fishery in waters off the west coast of Kamchatka (the most important king crab fishing area) was resumed in 1955, before the conclusion of the Japan-Soviet fishery treaty, and became subject to the provisions of the treaty in 1957, which covered two species of king crab, *P. camtschatica* and *P. platypus*. The regulations under the treaty were applied to both the Japanese and Soviet mothership fleets, with Japanese share decreasing since 1965. As a party to the 1958 continental shelf convention, the Soviet government declared, in 1968, its exclusive rights to natural resources of the continental shelf adjacent to its territory. Although Japan was not a member of the convention, she agreed, in 1969, to negotiate a separate arrangement for crab fishing, which resulted in a 1-year agreement specifying the catch limits of different species of crabs for the Japanese fisheries in designated areas, as well as the number of motherships or fishing vessels to be used for crab fishing. Thus, not only crab fishing on the west coast of Kamchatka for king crabs but also tanner crab fishing in the western Bering Sea, as well as fishing for a variety of crabs in waters off the southern Kuriles and Sakhalin became subject to regulation. The agreement has since been revised year after year. The complex legal arrangements for crab fishing in the northern North Pacific will later be reviewed in some detail.

TUNA FISHERIES

Japan had a tuna fishing fleet consisting of about 2,000 vessels before the war, but they were largely small boats operating in waters not too far from the home islands. Pole-and-line skipjack fishing was much more important than longline tuna fishing, with the bulk of the vessels carrying out both.[10] Skipjack fishing was also conducted from various bases in the present Trust Territory of the Pacific Islands. Although tuna are caught by other types of gear, particularly purse seine (also by traps in small quantities), the Japanese tuna industry consists largely of the longline tuna fishery and the pole-and-line skipjack fishery, the latter taking a sub-

[10] A complete account of the Japanese tuna industry up to about 1962 is given in Masuda (1963, in Japanese). In the Japanese language, skipjack ("katsuo") is distinguished from larger tunas ("maguro"). Substantial quantities of billfishes and swordfish are also caught by tuna longline; they are generally called "kajiki."

stantial amount of albacore also. While a number of vessels still conduct both types of fishing, distant-water tuna fishing is almost exclusively by longliners. The main grounds of the skipjack fishery are still in waters relatively close to the Japanese islands, including those adjacent to the Trust Territory of the Pacific Islands. In the licensing system of Japan, tuna and skipjack fisheries have always been combined, mainly because the tuna longline fishery originally developed as a part-time operation of skipjack pole-and-line vessels.

Under the new fishery law (1949), all tuna and skipjack vessels larger than 20 gross tons were required to obtain licenses issued by the Minister of Agriculture and Forestry, thus coming under full control by the central government. They were further divided between those below and above 100 gross tons, called the "medium vessel tuna-skipjack fishery" and the "far seas tuna-skipjack fishery," respectively. In 1953, after abolishment of the MacArthur Line, the Japanese government enacted a law to provide a preferential treatment of licenses for larger tuna vessels (over 70 gross tons) until 1955, as an attempt to develop tuna fishing in waters farther from the home islands. The law encouraged licensees to replace small vessels with new larger vessels and also accommodated the entry of operators from other fisheries, particularly the coastal trawl fisheries. A further policy was issued in 1955, allowing vessels in the category of the medium vessel tuna-skipjack fishery to combine their gross tonnages to obtain licenses for new larger vessels under the category of the "far seas tuna-skipjack fishery." A number of licenses were also transferred from the salmon fishery to the tuna fishery as the number of vessels in the former had to be reduced as a result of the Japan-Soviet fishery treaty.

Further changes were made thereafter to establish a new category for the mothership-type tuna fishery with deck-loaded catchers and to abolish the distinction between the above-mentioned two categories, with vessels less than 40 gross tons removed from the licensing system. As fishing by vessels less than 40 gross tons became free of license limitations, the number of such boats increased at a rapid rate with their fishing grounds expanded to both sides of the equator.[11] The government in 1963 put the licensing of tuna vessels over 20 tons again in two categories divided at 50 gross tons, which was later raised back to 70 gross tons. In short, the government encouraged the tuna fishery (particularly longline fishing) to expand into waters farther from Japan with larger vessels, and also used the tuna fishery for reducing the number of licenses in other overcrowded fisheries.

This policy contributed to the rapid expansion of tuna longline fishing grounds. By 1960, the Japanese tuna fleet had covered the main longline fishing grounds in the North and South Pacific and the Indian Ocean. Longlining in the Atlantic started in 1957 and the major Atlantic tuna grounds had been fished by 1962. Fishing grounds further expanded thereafter, though more gradually. Fishing for southern bluefin tuna ("minamimaguro," *Thunnus maccoyii*) in waters off New Zealand and southern Australia has been intensified greatly in recent years since new freezing equipment was introduced to produce frozen tuna meat of highest quality. The strength of the Japanese tuna longline fishery as a whole reached its highest point in 1962; the industry has been on the decline since then, with Taiwan and South Korea increasing their shares. Japan still has advantages over Taiwan and other longline fishing nations in some respects. It has a tremendous trade network developed by trade companies to market tuna anywhere in the world; the catches of many Taiwanese and South Korea longliners are transshipped through foreign bases under the management of these Japanese trade companies. High-quality bluefin is sold in Japan at a fantastic price. Japan also has strong markets for bigeye, billfishes, and other species that have no or very limited markets in the United States. But as far as tuna production is concerned, Japan's share will decrease further. In addition to Taiwan and Korea, Ryukyu has a sizable longline fleet, which will become part of the Japanese tuna industry when Okinawa is returned to Ja-

[11] In the Japanese practice, the actual gross tonnage of a vessel is substantially greater than the registered gross tonnage (RGT) in most cases.

pan. Cuba operates a small fleet in the Atlantic; the Soviet Union has a mothership tuna fishery of relatively minor importance. Most of the attempts by other nations to develop a tuna longline fishery have failed. (Venezuela has a fleet of small longliners. The fishery is protected by regulations prohibiting the import of tuna and tuna products.)

Tuna longlining is conducted in a variety of ways. The bulk of Japanese vessels still operate from Japan, but a large number also use foreign bases. In the South Pacific, catches are delivered to American Samoa, Espíritu Santo (New Hebrides), and Fiji. Penang and Port Louis (Mauritius) have been the main bases in the Indian Ocean. Mombasa is a base established recently. Vessels operating in the Atlantic have delivered their catches to such ports as Las Palmas, Abidjan, Cape Verde Islands (Portuguese possession), Tema, Cape Town, Port of Spain, etc. St. Martin Island in the Caribbean has been an important base in recent years. (See Broadhead, 1971, for a description of international tuna trade.) Many of these foreign transshipping bases now receive more fish from Taiwanese and Korean vessels than from the Japanese boats. Mothership-type tuna longlining has also been conducted both with self-navigating catchers and with deck-loaded boats, but the former type has ceased to exist. The mothership fishery with deck-loaded catchers has developed largely in the last 15 years although some experiments were conducted even before World War II. Each mothership, which also does fishing in most cases, carries 1 to 8 fishing skiffs. The catches of the different types of tuna fisheries are compared in Table 4.

It has been demonstrated that the catch per unit of effort in any region quickly decreases as the amount of longline fishing increases. It is also apparent that the total longline catches of yellowfin, albacore, bigeye, and bluefin tunas from the world ocean will not show substantial increases as fishing is further intensified although the proportions taken by the different longline fishing nations will change further.

The pole-and-line skipjack fishery operates relatively close to Japan, but a large number of vessels now fish in waters around the Trust Territory of the Pacific Islands (from bases in Japan). The fishery also takes a substantial amount of albacore; some vessels still conduct both pole-and-line skipjack fishing and tuna longlining.

Some tunas and skipjack are caught by purse seiners in waters close to Japan. A few tuna seiners have been operating in West Africa. The Japanese have also been trying to establish a purse-seine fishery in the eastern tropical Pacific, so far without success.

OTHER FISHERIES

Some of the other fisheries, principally those conducted around the Japanese islands, have had or are likely to have some international implications. These include, among others, the purse-seine fisheries for coastal pelagic fish, the saury fishery, and the squid fishery. The kelp fishery around the southernmost islands of the Kurile chain is also an international issue.

Most of these fisheries depend on the resources of coastal pelagic species in waters around Japan. The combined catch of main coastal pelagic species in *temperate waters*, including anchovy (*Engraulis*), sardines (*Sardinops* and *Etrumeus*), jack mackerels (mainly *Trachurus* and *Decapterus*), mackerels (two species of *Scomber*), saury (*Cololabis*), yellowtail (*Seri-*

TABLE 4.—Catches (metric tons × 10^3) of Japanese tuna fisheries.[1]

Years	Oceans			Longline					Pole-and-line[4]	Seine	Trap	Others
	Pacific and Indian	Atlantic	Total	Home-based	Foreign-based[2]	Atlantic	Mother-ship[3]	Total				
1962	395	55	450	275	23	55	51	404	21	16	3	6
1969	299	33	333	220	12	13	31	275	43	8	2	5

[1] Bluefin, southern bluefin, albacore, bigeye, yellowfin, and some small tunas.
[2] Other than Atlantic.
[3] With deck-loaded catchers.
[4] Mainly albacore.
Source: Ministry of Agriculture and Forestry (Japan) (1971).

ola), and common squid (*Ommastrephes*), was about 2.7 million metric tons in 1969[12] out of the total Japanese catch of all marine fishes and shellfishes of 7.7 million tons (round weight, not including aquaculture), indicating the importance of this group of species.

After the catastrophic decline of the sardine catch (Kasahara, 1961) fishing for other pelagic species, particularly those mentioned above, became increasingly intensive. Saury fishing with "boke-ami" (stick-held lift net with fish-attracting light) started in 1947, and the catch soon reached to a level of 500,000 metric tons a year. It has been on the decline since 1962 (Figure 4). The catch of jack mackerels started to climb sharply around 1949, with some signs of an increase in abundance, and exceeded 500,000 tons (*Trachurus* alone) in 1960; it has since been decreasing. The mackerel yield began to rise also in the late 1940's and it is still going up. The catch of anchovies has been fluctuating at around 300,000 to 400,000 tons a year since the early 1950's (Figure 5). The yield of squids, mostly common squid, also rose markedly after the war and has shown rather violent fluctuations in recent years (Figure 6). All of these species have been under intensive fishing for the last 20 years or so, but their catch trends have been rather different from each other. A variety of biological problems are involved, many of which are poorly understood. The catches of the Soviet Union and South Korea are also indicated in the figures wherever data are available.

The rapid development of fishing for mackerel and jack mackerel resulted in a serious conflict with the South Korean fishermen, which will be mentioned later. The Soviet vessels have been catching an increasing amount of mackerel in waters off northern Japan. The decline of the saury catch has prompted some of the Japanese companies to apply for exploratory fishing in waters of the eastern Pacific, particularly off Canada and the United States. In 1969, about 38 applications were approved by the Japanese government, but only about half of them conducted fishing, mainly off Canada and the United

[12] Perhaps 3 million metric tons if miscellaneous species are included.

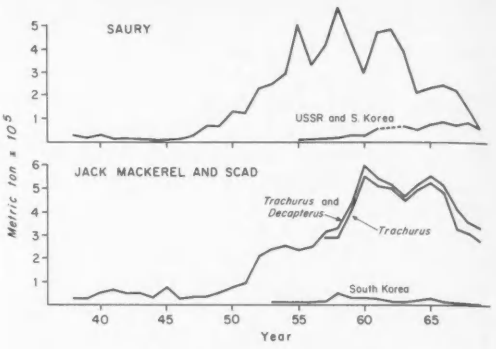

FIGURE 4.—Catches of saury and jack mackerel in Japan, 1938-69 (from Ministry of Agriculture, 1962-1971).

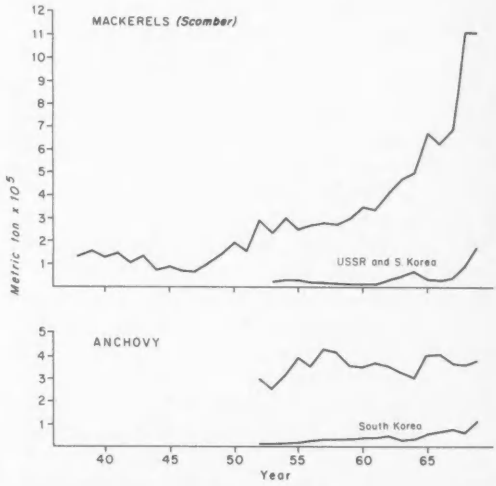

FIGURE 5.—Catches of mackerels and anchovy in Japan, 1938-69 (from Ministry of Agriculture and Forestry, 1962-71). USSR mackerel catches are only rough estimates.

States. The result was not very encouraging, but exploratory fishing will continue, depending to some extent on the saury catch in waters off Japan (there was a slight recovery in 1970) and the trend of the saury market. The Soviet catch of saury in waters off northern Japan and the Kuriles, in competition with the Japanese, has become substantial in recent years. A complicated international situation has developed con-

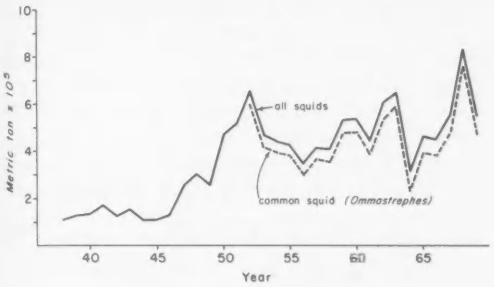

FIGURE 6.—Catches of squids in Japan, 1938-69 (from Ministry of Agriculture and Forestry, 1962-71).

cerning the Japanese kelp fishery in inshore waters around the southernmost islands of the Kurile chain occupied by the Soviet Union.

At the moment, squid fishing by Japan has no international implications, but the squid resources in the North Pacific appear to be among the most important potential resources for the future. Since species similar to the common squid occur in great quantities in the eastern Pacific, in waters of national jurisdiction as well as on the high seas, the exploitation of squid might become an international issue in the future. (A survey of squid resources off California is now under consideration in Japan.)

INTERNATIONAL ARRANGEMENTS

INTERNATIONAL PROBLEMS ARISING FROM THE POSTWAR EXPANSION OF JAPANESE FISHERIES

Period of Occupation

International conflicts arising from the prewar development of Japanese fisheries are summarized by Leonard (1944). Japan was involved in four major international issues concerning fisheries: the Russo-Japanese controversy; the North Pacific fur seal controversy; international problems of Antarctic whaling; and the Alaska salmon fishery issue. Except for the first one, which was resolved by the war itself, these controversies remained unsettled. The nature of the problems will be reviewed retrospectively in connection with postwar developments.

The Japanese fishing industry was half destroyed during the war with most of the larger fishing vessels sunk by American submarines. Large fisheries developed by the Japanese in Korea, Taiwan, Sakhalin, and the Kurile Islands were completely lost as these areas became independent or were taken by the Soviet Union. Japan also lost historical rights to fish in Kamchatka and other Far Eastern areas of the Soviet Union. The total catch decreased to less than 2 million metric tons in 1945, the last year of the war. The rebuilding of the industry started as early as 1946. Pressed by the immediate need to feed the nation and to earn foreign exchange, the government provided tremendous incentives for the industry to expand as fast as possible.

The first international problem faced by Japan was the area restriction imposed on her fisheries by the Allied Powers. Both government and industry strongly urged the expansion of the authorized fishing area. The area was expanded to the west to include a substantial portion of the east China Sea continental shelf (1946) and to the east and the south to permit tuna and skipjack fishing in vast areas of the western Pacific (1946, 1949, and 1950). As of 1950, however, the authorized area was still restricted to waters north of the equator and west of long 180°, except for Antarctic whaling, which was resumed in 1946.

Pressure was mounting in the United States and Canada to restrict Japanese high seas fishing as a condition for the restoration of diplomatic relations. Two international problems of the prewar period should be mentioned in this connection. During 1936-38, Japanese exploratory fishing vessels appeared in the eastern Bering Sea and caught salmon. This triggered tremendous reactions from the American industry, administration, and Congress. Legislation was introduced in Congress calling for the exercise of jurisdiction on the high seas, and a variety of views were expressed on the legal basis for taking such an action. The Japanese government finally agreed to keep its vessels from fishing salmon in waters off Alaska, without prejudice to Japanese rights under international law

(Leonard, 1944). The question of whether the United States had an exclusive right to exploit the salmon stocks was not discussed in legal terms, but the general feeling among the American people was that these salmon really belong to them. The above instance had a great impact on the attitude of the Americans toward the development of Japanese high seas fisheries after the war. Another prewar issue, which affected the reputation of Japan as a fishing nation, was the abrogation of the 1911 fur seal treaty by Japan.[13] The Japanese government claimed, without substantiating scientific evidence, that the increase in the fur seal population as a result of protection provided by the treaty was causing serious damage to their fisheries.

As the question of Japanese fishing became a very serious issue which might delay the conclusion of the peace treaty, the United States and Japan agreed to deal with problems further in an exchange of letters between the Japanese Prime Minister (Shigeru Yoshida) and the American Ambassador (John Foster Dulles) in February 1951. The prime minister's letter stated, ". . . the Japanese government will, as soon as practicable after the restoration to it of full sovereignty, be prepared to enter into negotiations with other countries with a view to establishing equitable arrangements for the development and conservation of fisheries which are accessible to the nationals of Japan and such other countries.

"In the meantime, the Japanese government will, as a voluntary act, implying no waiver of their international rights, prohibit their resident nationals and vessels from carrying on fishing operations in presently conserved fisheries in all waters where arrangements have already been made, either by international or domestic act, to protect the fisheries from over-harvesting, and in which fisheries Japanese nationals or vessels were not in the year 1940 conducting operations. Among such fisheries would be the salmon, halibut, herring, sardine, and tuna fisheries in the waters of the Eastern Pacific Ocean and Bering Sea." (Fishery Agency of Japan, 1953.)

[13] A notice was given in 1940 and the treaty terminated in 1941. To continue protective measures in the northeast Pacific, a provisional agreement was made between the United States and Canada.

The question of fur seal was dealt with in an exchange of memoranda in April 1951. The Japanese memorandum stated, "The Japanese government has no objection to the interpretation of Prime Minister Yoshida's letter of February 7, 1951, as extending to pelagic fur sealing. That is to say, pending the conclusion of a new convention on the subject after the coming into force of a peace treaty, the Japanese government will, implying no waiver of their international rights, voluntarily prohibit her nationals or vessels from carrying on pelagic fur sealing in the waters in question, and is moreover prepared to enter into negotiations toward the conclusion of a new convention."

Despite strong pressure from some sectors of the U.S. fishing industry, the United States government had managed not to include specific fishery articles in the draft peace treaty, except for Article 9 which set forth Japan's obligation to enter into negotiations with Allied Powers so desiring for the conclusion of bilateral and multilateral agreements on high seas fisheries. Negotiations for a tripartite fisheries convention between Canada, Japan, and the United States began on November 5, 1951, and were concluded on December 14. The Japanese delegation was shocked by the United States-Canada proposal for adoption of the abstention principle, which was an extreme form of resource allocation, not so much because Japan would have to refrain from fishing for North American salmon, halibut, and herring, but because of the potential effects of the adoption of such a principle on future fishery negotiations with other countries. Japan had no choice, however, and the treaty[14] was signed (on May 9, 1952) immediately after the entering into force of the peace treaty (April 28, 1952).[15] Except for those provided by the North Pacific fisheries convention, all restrictions on Japanese high seas fishing were removed.

[14] International Convention for the High Seas Fisheries of the North Pacific Ocean. The ratification of the treaty by Canada was delayed until 1953 due mainly to objections from the fishermen's union on the Pacific coast.

[15] Signed by 48 nations of the Allied Powers and Japan. Two separate peace treaties were signed, one with India and one with the Republic of China, both entering into force in 1952.

Implementation of the North Pacific Fisheries Convention

Since the establishment of the International North Pacific Fisheries Commission (INPFC) under the convention, two aspects of the implementation of the treaty provisions have been subject to intensive discussion between the representatives of the three governments: the possibility of moving the salmon abstention line (provisionally established at long 175°W) on the basis of scientific evidence and the question of whether the stocks on the abstention list continued to qualify for abstention. An enormous amount of research effort has gone into the study of the offshore distribution of all species of salmon, resulting in convincing evidence that a substantial portion of the North American salmon, particularly Bristol Bay sockeye salmon, enter the waters west of long 175°W and that, on the other hand, substantial numbers of Asian chum and pink salmon migrate into the waters east of long 175°W.[16] As the commission's recommendations have to be made unanimously, no action has been taken for moving the provisional line in either direction.

The convention provided that, during the initial 5-year period, no examination or recommendation be made as to whether the stocks continue to qualify for abstention. The period expired in 1958 and subsequent examinations of qualifications for abstention have resulted in some changes in the stocks on the abstention list. The following stocks have been removed from the list: the herring stocks off the coast of Alaska south of the Alaskan Peninsula and east of the meridian passing through the extremity of the Alaskan Peninsula; the herring stocks off the coast of the United States, south of the entrance to the Strait of Juan de Fuca; the herring stocks off the west coast of the Queen Charlotte Islands; and most important, the halibut stock of the eastern Bering Sea.[17]

[16] For the results of scientific investigations, see papers in Bulletins of the International North Pacific Fisheries Commission, for example, Margolis (1963), Kondo et al. (1965), Hartt (1966), Margolis et al. (1966), Neave, Ishida, and Murai (1967), Shepard, Hartt, and Yonemori (1968).

[17] While the removal of the herring stocks may have been partly to demonstrate the workability of treaty provisions, that of the Bering Sea halibut stock was an issue of practical importance to all parties.

The convention could be terminated by any one of the contracting parties serving 1-year notice after a period of 10 years, that is, June 1963. The Japanese government proposed negotiations for a new convention, which would eliminate the abstention principle, and such negotiations have been held several times since 1963, with no result. The United States and Canada would not consider abolishing the abstention principle. Japan, too, appears to have carried out negotiations more as a political gesture than a serious attempt to change the *status quo*.

The North Pacific Fisheries Commission has broadened its scope of operation to some extent by including serious discussions on the crab stocks in the eastern Bering Sea and the groundfish stocks in waters off the United States and Canada. In the earlier years, unofficial and temporary agreements were made as to the extent of Japanese fishing for groundfish in the Gulf of Alaska, as well as the way Japanese crab fishing is to be conducted in Bristol Bay. These aspects are now dealt with under separate bilateral, executive agreements between the two governments. The Commission has also been publishing results of research conducted by the national agencies of the three nations under its auspices, as well as fishery statistics on such stocks as salmon, halibut, herring, king crab, tanner crab, and groundfish.

In short, none of the parties have seriously considered abolishing arrangements under the treaty, particularly that for salmon. Both Canada and the United States seem to be satisfied that the treaty protects the North American salmon stocks just as well as any other international agreement that can realistically be conceived, while Japan appreciates the fact that, in years of large Bristol Bay sockeye salmon runs, a substantial quantity of North American salmon can be caught by Japanese fishermen. The only new problem faced by the commission is the entry of South Korean fishermen into salmon fishing in Bristol Bay—a development which might undermine the whole setup of the North Pacific fisheries convention. As South Korea is not a party to the convention, the commission has not been able to take any action except to

express its concern over the matter, and the issue has been handled mainly through direct negotiations between the United States and South Korea. The Japanese government has taken some action to prevent the involvement of Japanese companies in the Korean venture. The amount of salmon taken by the Koreans is still relatively small, perhaps in the order of several hundred metric tons in 1970, but if Korean fishing continues even at this rate it will seriously affect the stability of the salmon situation in the eastern North Pacific.

Japan-Soviet Salmon Controversy

Japan planned to send, in 1956, as many as 19 salmon motherships to the northwestern Pacific, including the Okhotsk Sea. The Soviet government issued, in February 1956, a unilateral declaration to restrict salmon fishing in waters west of long 170°E. There had been indications that the Soviet government might take some action to stop the phenomenal expansion of the Japanese high seas salmon fisheries.[18]

The Soviet declaration included: establishment, as an interim measure before the conclusion of an appropriate international treaty, of a salmon regulatory area covering the eastern Bering Sea, the northwestern Pacific and the Okhotsk Sea (Figure 7) to restrict salmon fishing (by both Soviet and foreign nationals) during the period of spawning migrations; establishment of a catch limit for 1956 at 50,000 metric tons; issuance, by the Soviet authorities, of licenses for fishing in the area; enforcement of regulations by the Soviet authorities; and the assurance that freedom of navigation in the area would not be affected. The action taken by the Soviet government was obviously related to negotiations for the normalization of diplomatic relations which had come to a deadlock just before the Soviet declaration on fishing.

[18] For example, at a meeting of the Economic Commission for Asia and the Far East (ECAFE) in 1955, the Soviet delegation pointed out that the salmon stocks in Kamchatka and other areas were in danger of being destroyed because of overfishing by Japan. Also, during negotiations for the normalization of diplomatic relations, which had been carried out in London, the Soviet representative stressed the need for restricting fishing for conservation of resources.

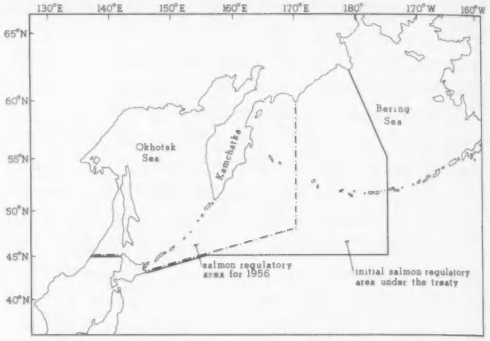

FIGURE 7.—Salmon regulatory area for the 1956 season and the initial salmon regulatory area under the 1956 treaty.

The Japanese government proposed immediate negotiations on fishery matters and sent to Moscow a team of top-notch experts headed by the Minister of Agriculture and Forestry. The convention, along with its protocol specifying regulatory measures and an agreement on emergency rescues, was signed on May 15. The treaty mentioned the maximum sustainable yield as the main objective, established the Japan-Soviet Fisheries Commission to consider joint conservation measures, set an annual salmon catch quota, and provided for enforcement of regulatory measures. The convention area was defined as the entire area of the northwest Pacific Ocean (excluding the territorial seas) including the Japan Sea, the Okhotsk Sea, and the Bering Sea. The protocol defined the regulatory area and spelled out regulatory measures to be taken for salmon, herring, and two species of king crab.

The convention provided that it would become effective upon entering into force of the peace treaty or the restoration of diplomatic relations. This undoubtedly speeded up peace negotiations, resulting in a joint declaration (to end the state of war and restore diplomatic relations) in December 1956. For all practical purposes, Japan's claim to the southernmost islands of the Kurile chain (which had been the main issue) was shelved. In order to permit Japanese salmon fishing for the 1956 season before the normalization of diplomatic relations, the two govern-

ments signed a temporary agreement which set a catch limit for that year. Japan undertook to reduce the size of the mothership fleet as a voluntary measure.

A lot of confusion occurred in connection with the procedure of obtaining licenses from the fishery inspection agency of the Soviet Ministry of Fisheries, but fishing did take place in the authorized areas in the Pacific and Okhotsk. Under the plan prepared before negotiations with the Soviet Union, 12 motherships with 375 catchers (including scouting boats) were to be sent to the northwestern Pacific and the western Aleutian waters, and 7 motherships with 213 catchers (including scouting boats) to the Okhotsk Sea. These were revised to 14 motherships with 447 catchers for the Pacific and Bering areas, and 2 motherships with 59 catchers for the Okhotsk Sea.

Since the regulatory area included part of the main fishing grounds of the land-based drift-net fishery, the total quota was divided into subquotas for the mothership fishery and the land-based fishery, each of which was further distributed among individual fishing vessels, establishing a precedent for an extremely detailed system of catch allocation. For the land-based drift-net fishery, quotas for individual vessels varied depending on their gross tonnage. The regulatory area under the temporary agreement did not cover vast areas to the east and south (Figure 7), and therefore a large amount (nearly one-half of the total take in 1956) was caught in waters outside. Due to delays in the issuance of licenses, the catch quota in the regulatory area was not filled within the established fishing period. The land-based longline salmon fishery, which began to develop in 1956, also took a considerable amount from waters outside the regulatory area.

The year 1957 was the first year of operation under the provisions of the convention. After hard negotiations both within and outside the fishery commission, the two governments settled for a total quota of 120,000 metric tons in the regulatory area, which now covered waters as far west as long 175°W but still excluded a substantial part of the land-based fishing grounds in the Pacific (see Figure 3 - Area A). The quota was divided, under Japanese regulations, between the mothership fishery and the land-based drift-net fishery and further among individual fishing vessels. The land-based drift-net fishery made more than one-half of their catch in outside waters, and the land-based longline fishery took twice the amount it caught in 1956, all from outside waters. The combined catch of all high seas salmon fisheries was about 162,000 metric tons as compared with the catch limit of 120,000 metric tons for the regulatory area. The 1958 agreement reduced the total quota to 110,000 metric tons which was again divided between the mothership fishery and the land-based drift-net fishery. Fishing in the Okhotsk Sea was further restricted, and a large closed area was established in waters off the east coast of Kamchatka.

Annual negotiations for salmon regulations have resulted in further restrictions on Japanese fishing. In 1959, the entire Okhotsk Sea was closed to high seas salmon fishing, and additional closed areas were established on the Pacific side. The catch quota for the regulatory area was further reduced to 85,000 metric tons, and a catch limit was set for sockeye salmon. In 1960, the Soviet Union proposed a southward expansion of the regulatory area to control fishing by land-based vessels carried out in outside waters. The Japanese undertook to take some domestic measures. The quota for the regulatory area has been reduced to 67,500 tons, with additional closed areas. A new step was taken in 1962 by designating the waters south of the previous regulatory area as Regulatory Area B, with the Japanese government undertaking to limit the catch in Area B to about 60,000 metric tons (with a 10% allowance). By then, the catch quota in the original regulatory area (now Area A) had been reduced to 55,000 tons. The Japanese government took a drastic measure to reduce the number of vessels both in the mothership fishery and the land-based drift-net fishery. Drift-net fishing in the Japan Sea was also reduced substantially. In 1964, the quotas were further reduced to 55,000 tons each for both Area A and Area B. Table 5 shows how the salmon catch

TABLE 5.—Japanese salmon catches by different fisheries compared with the total Soviet salmon catches. Catches are in metric tons $\times 10^3$.

Year	Japanese salmon catches					USSR total[1]
	Mothership	Land-based drift net	Land-based longline	Coastal traps and other fisheries	Total	
1956	93	41	8	9	151	160.0
1957	100	53	15	12	182	148.0
1958	92	74	16	14	196	71.0
1959	71	84	15	9	179	94.8
1960	54	67	17	9	147	71.0
1961	54	75	16	12	156	82.2
1962	45	42	15	15	116	61.8
1963	46	61	24	17	149	81.1
1964	44	45	12	16	117	46.9
1965	45	59	22	19	146	89.8
1966	39	50	21	16	127	59.7
1967	43	57	28	20	148	84.1
1968	38	51	13	12	114	39.2
1969	40	55	27	19	141	78.3

[1] Total of sockeye, pink, chum, coho, and chinook salmon.
Source of Japanese data: Ministry of Agriculture and Forestry (Japan) (1962-71).
Source of Soviet data: FAO Yearbook of Fishery Statistics and Kasahara (1963).

has been shared by different fisheries since 1956[19] (see Figure 3 for the fishing grounds of various fisheries). Although the details of changes in regulatory measures under the convention have not been mentioned, the above review clearly indicates that the Japanese high seas salmon fisheries have been subject to an increasing amount of control. The table also compares the Japanese catches (including small amounts of salmon destined for Japanese streams) with the Soviet catches.

Annual negotiations between the two governments both within and outside the commission have been very political, and in most cases important decisions have been made toward the end of each year's session as political compromises. From the data and information exchanged through the commission, it is difficult to evaluate the status of each of the important salmon stocks, particularly because the origin of much of the fish taken in offshore waters is not identifiable (except for such stocks as Karaginski pink salmon which to a large degree remain separate from others in their offshore distribution). The fact that the Japanese mothership fishery takes a large amount of Bristol Bay sockeye salmon in some years further complicates the situation.

The possibility of Korean fishermen conducting high seas salmon fishing in the Japan-Soviet treaty area has posed a problem which is substantially different from the question of Korean entry in the eastern Pacific. The Soviet Union has unofficially indicated that, if that happened, any amount of salmon Korea might take would have to be subtracted from the quota for the Japanese fisheries. Korean salmon fishing has not developed as yet, perhaps for two reasons: First, lacking diplomatic relations with the Soviet Union, their fishing vessels might be seized and fishermen jailed by the Soviet authorities if the Soviet government should take a strong stand, and there would be no way of settling the problem through negotiations, nor would any of the nations bordering the North Pacific take a sympathetic attitude toward South Korea. Second, the Japanese government and industry might take retaliatory measures such as more severe restrictions on sea food import from Korea.

[19] A 2-year cycle due to pink salmon fluctuations is obvious. This has been taken into account when setting quotas.

North Pacific Crab Controversies

International problems arising from king crab fishing after World War II are rather unique in several respects. Japan, the Soviet Union, and the United States have all been fishing for king crab, with Japan and the Soviet Union operating distant-water fisheries. While all three states fish for crab in the eastern Bering Sea, there has been no tripartite agreement dealing with crab fishing, international problems

being handled under three separate bilateral agreements, Japan-Soviet, United States-Japan, and United States-Soviet. Two of the three states, the Soviet Union and the United States, are parties to the 1958 continental shelf convention, which came into force in 1964, while Japan is not. The Soviet Union and Japan have developed a unique system to allocate tangle-net fishing grounds between their mothership fisheries both in Kamchatka and in the eastern Bering Sea.

As has been mentioned in the section on Review of Selected High Seas Fisheries, Japan planned to resume the mothership crab fishery during the 1952 season but did not proceed with the plan in fear of political repercussions from the United States. The fishery began in 1953 with one mothership jointly operated by the three biggest companies, each taking an equal share of interest and obligation, with a production quota of 50,000 cases (one case equals 48 cans of one-half pound each) set by the Japanese government, along with various restrictions on the fishing area and gear. This pattern of operation continued until 1956, when the production quota increased to 57,000 cases (plus some allowance). There were some U.S. crab vessels (trawlers) fishing in Bristol Bay from time to time, and arrangements were made for minimizing gear conflicts, but the U.S. catch was very small then. The rapid expansion of the Japanese crab fishery in Bristol Bay began in 1959, when the quota was raised to 70,000 cases. It was further increased to 80,000 cases in 1960, and in the same year a new mothership operation was authorized under an exploratory fishing license.[20] The Soviet crab fishery in Bristol Bay also started this year with one mothership. Thereafter expansion continued at an increasing rate.

By 1962, the fishery had grown to include three motherships in the spring season and two in the autumn. In 1963, the government consolidated the operations of different motherships and authorized only two, each managed jointly by several companies, with a total production quota of 235,000 cases (including frozen meat at a conversion rate of 100 tons of crab meat to 10,000 cases). The Soviet Union sent three motherships to the same area, resulting in some incidents of gear damage. During the period of expansion, the United States and Japan conducted research on the king crab stock in the eastern Bering Sea as part of the INPFC program, and the United States repeatedly expressed its concern over the condition of the stock.

In 1964, the United States enacted a law to prohibit exploitation of resources of its continental shelf by foreign nationals (the Convention on the Continental Shelf was ratified by the United States in 1961 and came into force in 1964). In a statement by the President, however, the United States indicated that due consideration would be given to the historical interest of Japan in king crab fishing in the eastern Bering Sea. Official negotiations were carried out during October-November 1964. As expected, Japan held the view that the king crab stock under question was a high seas resource, while the United States claimed the stock as a resource of the continental shelf over which the coastal state had exclusive jurisdiction. Although there was no agreement on the legal basis for regulating the exploitation of the stock, the two governments agreed to take certain measures for the seasons 1965 and 1966, including a reduction of the quota for the Japanese fisheries to 185,000 cases and various conservation measures applicable to the nationals of both nations. Fishing gear other than the tangle net and the pot was prohibited, and a large area was reserved exclusively for pot fishing.

A second round of negotiations was held in late 1966 and the agreement was extended, with the Japanese production quota further reduced to 163,000 cases for 1967-68. The agreement was revised again in 1968 for another 2 years, reducing the Japanese quota to 85,000 cases on the ground that the condition of the stock was deteriorating. For the first time, the need for paying attention to the condition of the tanner crab stock was discussed, and the Japanese government set a catch limit for tanner crab for the season 1969.

[20] The catch was processed to frozen crab meat, with a production quota of 180 tons. Fishing was conducted with three deck-loaded boats and one independent boat.

The U.S. government began negotiations with the Soviet Union for regulating crab fishing in the eastern Bering Sea. In this case, both governments were parties to the continental shelf convention and recognized the king crab stock as a resource of the U.S. continental shelf. An agreement was signed to limit the Soviet king crab production in the eastern Bering Sea to 118,600 cases for the seasons 1965 and 1966. The agreement has been revised from time to time since then, resulting in a continuous reduction of the Soviet quota, to 52,000 cases for 1969-70. The tanner crab catch was also limited to 40,000 cases per year for the same seasons.

The United States also suggested that there be a system of allocating tangle-net crab grounds between the Japanese and Soviet fleets, which would be similar to one implemented in Kamchatka for some time. Negotiations between the three governments were held in 1967, resulting in an arrangement shown in Figure 8. The agreement was renewed for 1969-70; the area reserved for pot fishing was expanded, and the remaining grounds for tangle-net were divided between the fleets of the two nations again. The allocated fishing strips have been rotated annually between the Soviet Union and Japan (there are many practical problems under this arrangement, including the use of fishing lots after the fleet of one nation has left).

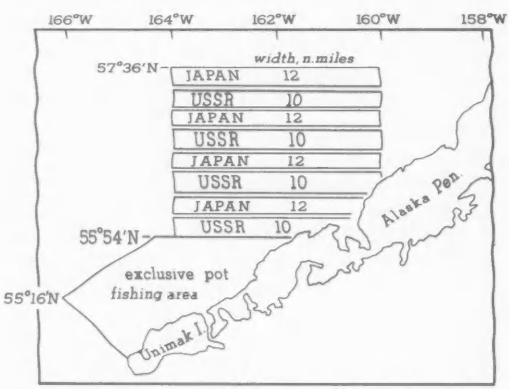

FIGURE 8.—Allocation of king crab fishing grounds in the eastern Bering Sea, 1969 (from Suisan-sha, 1970).

In short, a system of allocation has been developed between the three nations for crab fishing in the Bering Sea. Japanese fishing has been subject to catch limits under a United State-Japan agreement, which is legally not based on the continental shelf convention; Soviet fishing has been subject to catch limits under a Soviet-United States agreement which is based on the continental shelf convention; U.S. fishing has not been subject to catch limits; the Japanese and the Soviet quotas have been reduced, while the U.S. catch has increased rapidly in the last few years; a large area has been allocated exclusively for pot fishing; the tangle-net fishing area has been divided between the Japanese and Soviet fleets and rotated annually; size limits and other conservation measures have been applied to all nations. These arrangements have been made through executive agreements, and not by treaties requiring ratification.

On the Asian side, Japanese crab fishing in waters off the west coast of Kamchatka was resumed in 1956. The government authorized two motherships, each operated jointly by two companies, with a production quota of 60,000 cases each (plus 5% allowance), which was increased to 70,000 during the fishing season. Four motherships operated in 1956, with a production quota of 70,000 cases each (plus allowance). The actual production reached 313,000 cases.[21] The Japan-Soviet fishery convention, which entered into force in late 1956, included regulatory measures for two species of king crab (*P. camtschatica* and *P. platypus*), but the Japan-Soviet fisheries commission did not restrict fishing effort or the catch during the season 1957. At the annual meeting of the commission in 1958, the Soviet Union stressed the need to restrict crab fishing, and each government undertook to take certain measures (not as commission's decisions but as actions by each government), including a limitation on the number of motherships (no more than four Japanese motherships for 1958-60 and six Soviet motherships for 1958) and production quotas (no more than 320,000 cases per

[21] The government also authorized one mothership to operate in the Olyutorski area, but the fleet could not reach its production quota. The unfilled portion of the quota was taken by one of the four motherships operating in west Kamchatka.

year by Japan for 1958-60 and 480,000 cases by the Soviet Union for 1958). The commission recommended to close waters south of lat 53°N, and the Soviet government undertook to take a similar measure for fishing within its territorial sea. The national quotas for mothership fisheries were further reduced in 1959 to 280,000 cases for Japan and 420,000 cases for the Soviet Union. Various other measures also took effect to restrict fishing and avoid conflicts. Further changes were made thereafter to increase the proportion of the Soviet share in the total mothership catch and to reallocate fishing grounds between the fleets of the two nations (Figure 9), with the Soviet Union taking somewhat wider strips.

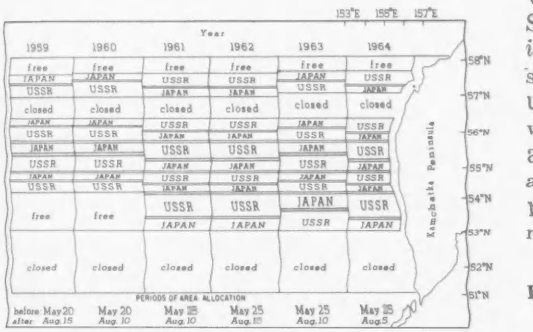

FIGURE 9.—Allocation of king crab fishing grounds off west Kamchatka, 1957-64 (from Norin Keizai Kenkyusho, 1965).

A new situation developed in 1968 when the Soviet government declared sovereign rights to the resources of the continental shelf and wished to enter into negotiations in 1969 for a separate agreement for crab fishing. As in the case of United States-Japan negotiations, Japan refused to recognize the Soviet claim not only on the ground that Japan was not a party to the continental shelf convention (the Soviet ratified the continental shelf convention in 1960) but also for the reason that she did not consider the crab a continental shelf resource. The fact that Japan is not a party to the convention might not have been considered a strong enough reason for arguing against the Soviet claim since the convention had been ratified by most of the major fishing nations. After prolonged negotiations, an agreement (in the form of an exchange of letters, along with a protocol and agreed minutes) was reached by shelving the positions of the two governments on legal questions.

Thus, the numbers of vessels (motherships or land-based vessels) were limited and the catch quotas (in terms of either canned crab produced or the number of crabs caught) established for *P. camtschatica* in west Kamchatka; "ibara crab" (a deepwater crab, *Lithodes aequispina*) in west Kamchatka; tanner crab in the western Bering Sea (off the Gulf of Anadyr and waters between Cape Olyutorskiy and Cape Govena); tanner crab, *P. camtschatica*, and *P. platypus* ("abura crab") in waters off the east coast of Sakhalin; hair crab (*Erimacrus*) and *P. brevipes* ("hanasaki crab") in waters around the southernmost islands of the Kurile chain (Figure 10).[22] Fishing grounds for all these fisheries were specified, and closed seasons, size limits, and various other restrictions applied. The Japanese government issued a new set of domestic regulations to cover these fisheries. Quotas for most areas were further reduced in 1970.

Fur Seal Convention

As mentioned above, Japan undertook, during the occupation period, to voluntarily prohibit her nationals or vessels from carrying on pelagic fur sealing, pending the conclusion of a new convention. Negotiations for a new convention took a number of years, and the convention signed in 1957 (came into force the same year) was called an Interim Convention for the Conservation of North Pacific Fur Seals. Although it is

[22] Japan had developed a substantial mothership fishery for *P. platypus* in waters along the coast of Olyutorskiy. This fishery was terminated by the 1969 crab agreement on the ground that the stock had been depleted. The remaining part of the crab fishery in that region was mainly for tanner crab in waters east of Cape Navarin and west of Cape Olyutorskiy conducted by motherships and land-based vessels. Japanese tanner crab fishing in waters off the west coast of Sakhalin and Primore (the Soviet mainland coast of the Japan Sea) was also terminated with the fishing vessels transferred to the tanner crab grounds along the east coast of Sakhalin.

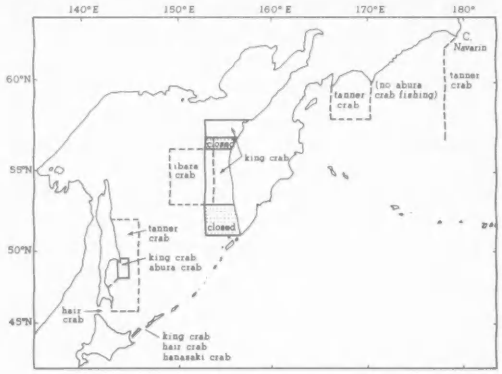

FIGURE 10.—Crab fishing regulated under the Japan-USSR crab agreement, 1969 (from Suisan-sha, 1970).

still called an interim convention, it is almost a permanent arrangement. Pelagic sealing is prohibited; a system of product distribution more or less similar to that under the 1911 convention is in effect. While the previous convention carried out its tasks without forming an international body, the new one established an international commission. Much emphasis has been placed on a research program to arrive at an optimum level of harvesting and examine the effects of seal predation on other fishery resources.

Rhee Line

Perhaps the most difficult fishery controversy Japan has ever faced is the Rhee Line issue arising from a declaration by President Syngman Rhee of the Republic of Korea concerning marine sovereignty. Korea had ceased to be a Japanese colony at the end of the war, and negotiations for normalizing relations between the Republic of Korea (South Korea) and Japan began in February 1952 and continued until June 1965, for a period of 13 years. The most difficult of all the problems was the fishery dispute. The seizure of Japanese fishing vessels by Korean authorities for alleged violation of waters under Korean jurisdiction started as early as 1947, immediately after the postwar expansion of Japanese fisheries began, and incidents increased greatly in the following few years. On January 18, 1952, President Syngman Rhee issued a declaration claiming sovereign rights to all natural resources over a vast area delimited by the so-called Rhee Line (Figure 11).[23] On September 8, 1953, the Korean government further issued a statement ordering all Japanese fishing vessels to stay outside the line, and enforced the order strictly at the height of the Japanese mackerel fishing season. Four major Japanese fisheries were affected: the pole-and-line mackerel fishery (with lights), the purse-seine fishery for jack mackerel, the trawl fishery west of long 130°E, and, least important, the trawl fishery east of long 130°E. Between 1947 and 1959, 326 Japanese fishing vessels were seized and the bulk of the 3,900 fishermen involved were jailed (of these, 141 vessels and practically all fishermen were returned later). The Japanese government did not contest the Korean claim by force but merely tried to minimize the number of incidents by running her patrol boats along the Rhee Line.

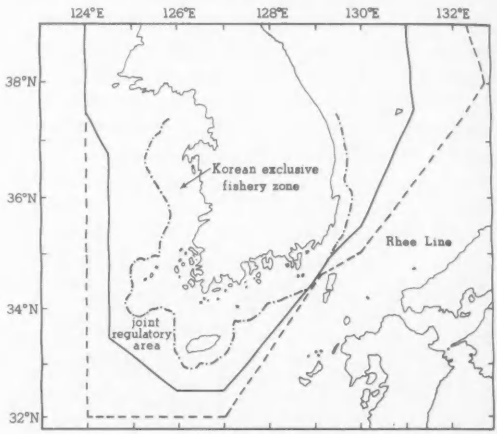

FIGURE 11.—Korean exclusive fishery zone and the joint regulatory area under the Japan-Korea fishery agreement (from Fishery Agency, 1965). Large portions of the joint regulatory area are closed to trawl fishing.

[23] The preamble of the declaration referred to established international precedents, and the Truman proclamations of 1945 were mentioned in this connection.

Among the issues taken up during negotiations for the normalization of diplomatic relations, the treatment of property claims and the conclusion of a fishery agreement were most difficult, and the fishery dispute perhaps created far more problems than the claim issue, for it affected the operations of thousands of Japanese vessels. (Among the other main agenda items were the establishment of basic relations between Japan and the Republic of Korea, the laying of submarine cables, and the conclusion of a treaty concerning trade and navigation.) The final settlement reached in June 1965 included four agreements, of which one on property claims and economic cooperation and one on fisheries were the most important from a practical point of view. The former specified the forms and amounts of monetary compensations. Japan undertook to provide $300 million (360 yen per dollar) as grants, $200 million as government loans (at 3.5% with a repayment period of 20 years including 7 years of grace),[24] and more than $300 million of commercial credit at a low interest rate. A substantial portion of the total sum was expected to be spent for fishery development, mainly in the form of vessels and equipment.[25]

The agreement between Japan and the Republic of Korea concerning fisheries consisted of the mutual recognition of a right to establish a 12-mile fishery zone over which the respective coastal state would have exclusive fishery jurisdiction, and the establishment of a joint regulatory area in which fishing by the nationals of both nations was to be restricted as to the numbers, sizes, and types of fishing vessels as well as the annual catches of the fisheries concerned. Closed areas, closed seasons, and other restrictions were also applied. The Korean exclusive fishery jurisdiction zone and the joint regulatory area established under the agreement are shown in Figure 11. Japan established a 12-mile fishery zone along the coast facing Korea. Arrangements under the agreement, its protocol, and subsequent agreements are extremely complex.

The effects of the fishery agreement have been quite remarkable. Disputes over fishing activities have ended almost completely.[26] No major controversies have developed from the annual meetings of the Japan-Korea fisheries commission established under the agreement. During the period of negotiations, the Korean fishing industry had grown to a strong competitive industry which no longer needs much legal protection against Japanese fishing activities. It is obvious that, on a give-and-take basis, Korea gained much more than she gave up in the overall settlement, which to a large extent depended on the resolution of fishery disputes. The fishery agreement and its protocol also indicate how far the Japanese government might go in making complicated arrangements to settle international fishery problems.

Conflicts with People's Republic of China

After the outbreak of the Korean War, Japan began to have serious problems with the People's Republic of China.[27] During 1951-54, more than 150 vessels, practically all pair trawlers, were seized in the East China Sea by the Chinese patrol vessels (Norin Keizai Kenkyusho, 1965). Negotiations began in 1954 between a Japanese nongovernmental organization and a Chinese fishery association, resulting in a 1-year agreement on the operation of the trawl fishery in the East China Sea (including the Yellow Sea). The coastal areas were closed to trawl fishing, and the numbers of Japanese and Chinese trawl vessels to operate in certain areas during certain periods were limited. The agreement was extended for another 2 years but was terminated by China in 1958, resulting in another outbreak of incidents. A separate agreement was made in 1959 concerning emergency port calls by

[24] Loans may be used for both capital goods and material.

[25] The Korean government originally envisaged investing roughly $150 million in fishery development, but actual items to be provided by Japan have been negotiated annually.

[26] Most of the fishery problems since the conclusion of the treaty agreement have been in connection with the export of Korean fishery products to Japan, particularly dry laver, the only export market of which is Japan who also has a very large laver aquaculture industry.

[27] Although Japan was not involved in the war, she provided bases close to Korea and was also an important source of war supplies.

fishing vessels (each side designated three ports for emergency calls). Negotiations for another fishery agreement began in 1963, and the previous agreement was revived with certain modifications for another 2 years. The agreement has since been revised and modified from time to time. Under the agreement signed in June 1970, the Japanese delegation agreed to enter into negotiations with a view to restricting purse-seine fishing. A new agreement was signed in December 1970 establishing three regulatory areas for purse seining: one is closed and the numbers of Japanese and Chinese seiners are limited in the remaining two.

Although these agreements have helped reduce the number of incidents greatly, their nongovernmental status made it difficult for Japan to enforce the agreed regulatory measures, and many violations have occurred. The important stocks of groundfish in the East China Sea are generally in poor condition due to overexploitation. There is no way of developing an overall international agreement to protect and allocate these resources, for diplomatic relations do not exist among some of the countries exploiting the same stocks. China has taken the greatest proportion of the total landings, although no reliable estimate is available. Japan's catch has been substantial, while the proportions taken by South Korea, North Korea, and Taiwan have been relatively small.

Extension of Limits of National Jurisdiction

Japan has been dealing with an increasing number of problems arising from the extension of the limits of national jurisdiction through unilateral claims by coastal states. As a general trend is for more nations to claim broader zones, a review of Japan's responses to these claims is appropriate.

United States.—Except for the abstention provisions of the North Pacific fisheries treaty, the Japan-United States crab agreement, and regulatory measures recommended by INPFC for Bering Sea halibut, Japanese fisheries in the eastern half of the Pacific Ocean have been relatively free of restrictions. The Japanese government initially controlled the expansion of groundfish fishing into waters south of the Alaskan Peninsula on the basis of unofficial discussions with the United States, but the situation changed in 1965 when the government issued regular licenses to a substantial number of vessels.

Negotiations for resolving problems arising from the establishment of an exclusive fishery jurisdiction zone by the United States in 1966 (3-12 miles) began in January 1967, and an agreement came into effect in May 1967. While the United States took the position that an exclusive fishery zone could be established by a domestic law, Japan held the view that such a zone had no legal basis without an international agreement. As in the case of the crab dispute, the governments shelved their legal positions and worked out practical arrangements.

The agreement covered a wide variety of fishing activities, both within and outside the fishery zone. For example, Japan was permitted to continue the established fisheries within the fishery zone for crabs off the Pribilof Islands, groundfish along the Aleutians except during certain periods in certain areas, whales along the Aleutians and the Gulf of Alaska except between long 150°W and 163°W, salmon off the Aleutian Islands west of long 175°W, and tunas except in waters around the Hawaiian Islands and off the mainland coast. Certain areas within the zone were also designated for loading and support activities. In turn, Japan undertook to refrain from fishing in certain areas of international waters during the first part of the halibut season and during the main crab pot fishing season. The agreement has since been revised twice, the most recent revision (effective January 1971) being summarized in Figures 12 and 13. (In comparison, the United States-Soviet agreement is summarized in Figures 14 and 15.)

It is obvious that the United States has tried, with some success, to reduce the effects of foreign fishing in international waters on important domestic fisheries in turn for allowing foreign fishermen to continue their fishing in areas within the exclusive fishery zone where such fishing does not seriously affect domestic fisheries. The United States has also avoided con-

U.S.S.R.
CANADA
JAPAN PERMITTED LOADING WITHIN CONTIGUOUS ZONE OFF:
1. SANAK ISLAND
2. SEMIDI ISLANDS
3. KAYAK ISLAND
4. FORRESTER ISLAND
5. AFOGNAK ISLAND
JAPAN PERMITTED LOADING WITHIN CONTIGUOUS ZONE OFF ST. MATTHEW ISLAND
JAPAN PERMITTED TRAWLING, LONGLINING, CRABBING, AND LOADING WITHIN CONTIGUOUS ZONE OFF ST. GEORGE ISLAND
JAPAN PERMITTED TRAWLING, LONGLINING AND LOADING WITHIN CONTIGUOUS ZONE DECEMBER 1 THRU MAY 31
JAPAN WILL REFRAIN FROM TRAWLING IN INTERNATIONAL WATERS IN THESE ZONES DURING FIRST 5 DAYS OF THE HALIBUT SEASON
JAPAN WILL REFRAIN FROM TRAWLING AND LONGLINING IN INTERNATIONAL WATERS IN THESE ZONES:
1. AUGUST 20 THRU APRIL 30
2. MAY 7 THRU MAY 21 OR FIRST 15 DAYS OF HALIBUT SEASON
3. SEPTEMBER 15 THRU FEBRUARY 15
JAPAN PERMITTED WHALING WITHIN CONTIGUOUS ZONE EXCEPT BETWEEN LONG 163°W AND LONG 150°W
JAPAN PERMITTED LOADING WITHIN CONTIGUOUS ZONE OFF UNALASKA ISLAND
JAPAN PERMITTED TRAWLING, LONGLINING AND LOADING WITHIN CONTIGUOUS ZONE:
1. YEAR-ROUND
2. APRIL 1 THRU OCTOBER 31
3. YEAR-ROUND
4. FEBRUARY 16 THRU SEPTEMBER 14
Prepared March 1971
National Marine Fisheries Service
Juneau, Alaska

FIGURE 12.—Arrangements under the United States-Japan fishery agreement (December 1970) concerning the U.S. contiguous fishery zone, off Alaska (taken from Commercial Fisheries Review, 1971a).

FIGURE 13.—Arrangements under the United States-Japan fisheries agreement (December 1970), off the Pacific Northwest (taken from Commercial Fisheries Review, 1971a).

cluding a long-term agreement which might affect her position with respect to global negotiations now being held.

Mexico.—When Mexico declared, in 1967, a 3-mile exclusive fishery zone beyond her 9-mile territorial sea, Japan entered into negotiations with Mexico to protect her vested interest in tuna longline fishing in waters between 9 and 12 miles. There was no agreement on the legality of the Mexican claim, but practical arrangements were worked out so that, except in areas particularly important to sport fishing, Japan was able to continue longline fishing in waters between 9 and 12 miles without exceeding the amount of effort in the previous years. The agreement was in the form of an international treaty effective over a period of 5 years. This was a relatively minor dispute.

New Zealand.—New Zealand declared a 9-mile exclusive fishery zone beyond her 3-mile territorial sea in 1966. Japan entered into negotiations with New Zealand to protect her longline porgy ("tai") fishery within the newly claimed area. The agreement reached in 1967 allowed Japanese fishing to continue in waters between 6 and 12 miles without increasing the number of vessels, nor their size, until the end of 1970 (for 5 years after the establishment of the exclusive

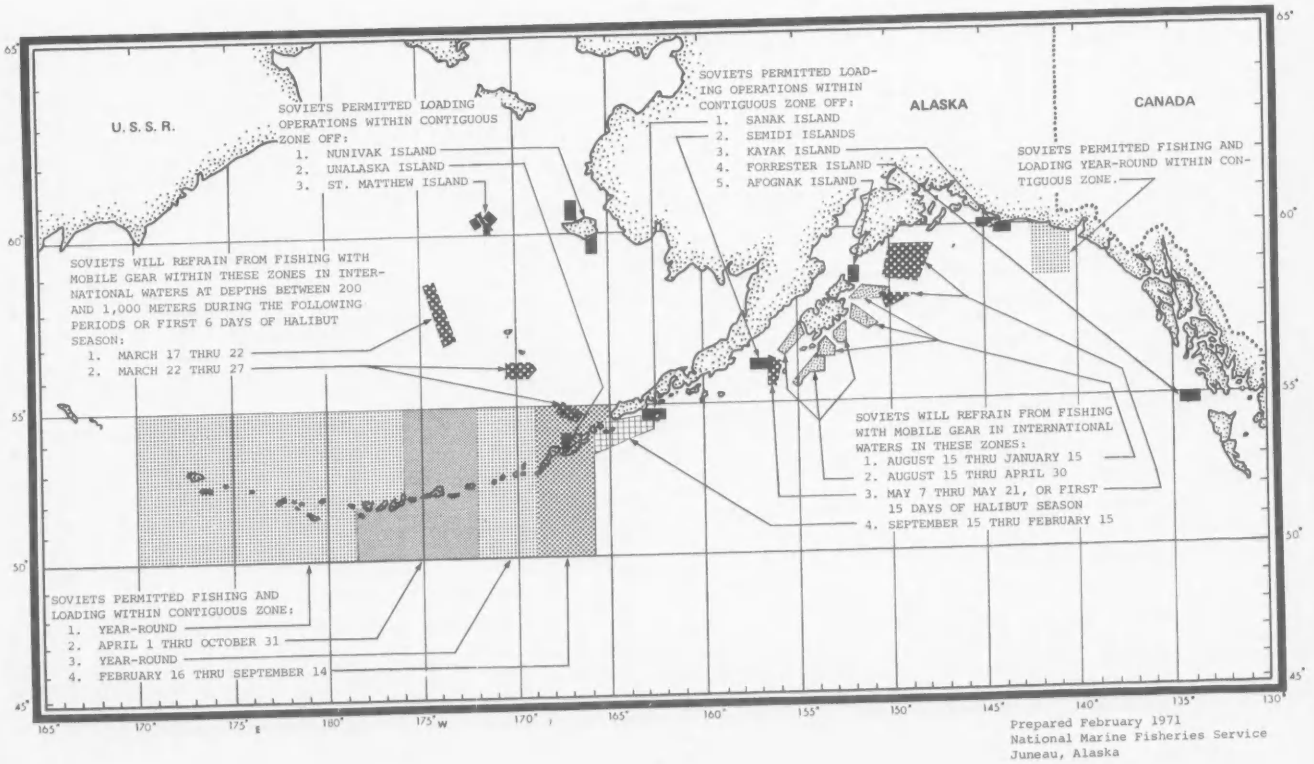
U. S. S. R.
SOVIETS PERMITTED LOADING OPERATIONS WITHIN CONTIGUOUS ZONE OFF:
1. NUNIVAK ISLAND
2. UNALASKA ISLAND
3. ST. MATTHEW ISLAND
SOVIETS PERMITTED LOADING OPERATIONS WITHIN CONTIGUOUS ZONE OFF:
1. SANAK ISLAND
2. SEMIDI ISLANDS
3. KAYAK ISLAND
4. FORRESTER ISLAND
5. AFOGNAK ISLAND
ALASKA
CANADA
SOVIETS PERMITTED FISHING AND LOADING YEAR-ROUND WITHIN CONTIGUOUS ZONE.
SOVIETS WILL REFRAIN FROM FISHING WITH MOBILE GEAR WITHIN THESE ZONES IN INTERNATIONAL WATERS AT DEPTHS BETWEEN 200 AND 1,000 METERS DURING THE FOLLOWING PERIODS OR FIRST 6 DAYS OF HALIBUT SEASON:
1. MARCH 17 THRU 22
2. MARCH 22 THRU 27
SOVIETS WILL REFRAIN FROM FISHING WITH MOBILE GEAR IN INTERNATIONAL WATERS IN THESE ZONES:
1. AUGUST 15 THRU JANUARY 15
2. AUGUST 15 THRU APRIL 30
3. MAY 7 THRU MAY 21, OR FIRST 15 DAYS OF HALIBUT SEASON
4. SEPTEMBER 15 THRU FEBRUARY 15
SOVIETS PERMITTED FISHING AND LOADING WITHIN CONTIGUOUS ZONE:
1. YEAR-ROUND
2. APRIL 1 THRU OCTOBER 31
3. YEAR-ROUND
4. FEBRUARY 16 THRU SEPTEMBER 14
65°
60°
55°
50°
45°
165°
170°
175° E
180°
175° W
170°
165°
160°
155°
150°
145°
140°
135°
130°
Prepared February 1971
National Marine Fisheries Service
Juneau, Alaska

FIGURE 14.—Arrangements under the United States-USSR fisheries agreement (February 1971), off Alaska (taken from Commercial Fisheries Review, 1971b).

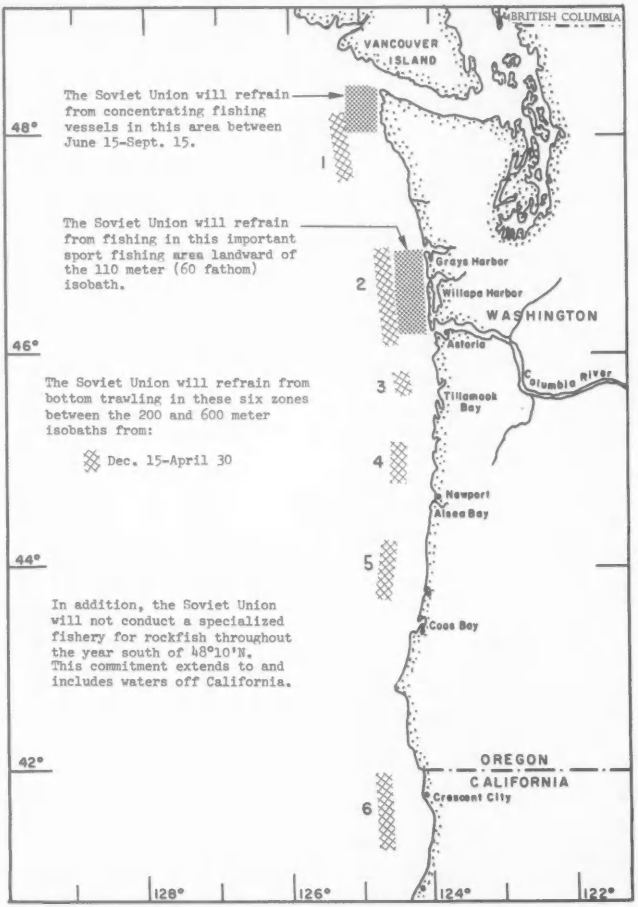

FIGURE 15.—Arrangements under the United States-USSR fisheries agreement (February 1971), off the Pacific Northwest (taken from Comemrcial Fisheries Review, 1971b).

fishery zone in January 1966). Japanese fishing within the zone terminated at the end of this period.

Australia.—Australia declared, in 1968, a 9-mile exclusive fishery zone beyond her 3-mile territorial sea (including Territory of Papua), and at the same time indicated that Australian ports would in principle be closed to foreign fishing vessels. The Japanese tuna longline fishery, mainly for southern bluefin, would be affected, especially by the closure of ports. Tuna vessels would have to pay license fees to fish in the exclusive fishery zone. Negotiations took over 3 months. As usual, the question of legality of the claim was shelved, but the agreement reached envisaged the phasing out of Japanese fishing in 7 years. Australia designated four ports for Japanese tuna vessels to visit, each paying a small fee.

Indonesia.—In 1957, Indonesia claimed all waters within her archipelago as internal waters and started seizing Japanese tuna boats, particularly in the Banda Sea, which was an important tuna fishing area for smaller longliners. An

agreement was concluded, in 1968, between the Japanese industry (represented by the Federation of Japan Tuna Fishery Co-operatives and the National Federation of Fishery Co-operatives) and the Indonesian Ministry of Agriculture. The number of vessels to operate in the Banda and Ceram Seas was limited for each of the three size categories (most of the vessels being less than 70 gross tons) with a maximum total number of 250 vessels and an annual quota of 15,000 metric tons. Each vessel was to pay a sum of money for using Ambon as a supply base. A substantial amount of technical assistance was also to be provided by Japan in connection with the agreement. The agreement was for a period of 1 year, but has been renewed every year with minor changes.

West Africa.—The Japanese trawl fishery along the coast of West Africa has been facing increasing difficulties due to the extension of the territorial sea and other unilateral claims by the coastal states (see Table 6 for present status). Fishing in the northern area, along the coast of Spanish Sahara and Mauritania for cuttlefish, octopus, and porgies, has been affected seriously by the estabishment of an exclusive fishery zone (6-12 miles) by Spain and the extension of the territorial sea by Mauritania. In the case of Mauritania, an extensive straight base line measuring some 90 nautical miles was used along the northern part of its coast. Both governments enforced these measures and seized some Japanese vessels.

While Spain has not agreed to negotiate with Japan on fishery problems arising from her action, Mauritania did. After a long period of negotiation, a 1-year agreement was signed in February 1970 (came into effect in April 1970) which might be extended for another year with the consent of both parties. It provided for 24 Japanese trawlers to operate within the 12-mile zone, plus 5 small vessels within 3 miles of the coast. The latter vessels would deliver their entire catch to Mauritania, which would then be sold to Japan. Each of the 24 trawlers would provide training for three Mauritanian fishermen, and each of the five small vessels for one fisherman. Japan also undertook to purchase fish taken by local Mauritanian fishermen. Although Japan would pay a certain sum (approximately $28 per gross ton of each vessel per year), Japan did not want to have it called "a fishing fee." As far as Japan was concerned, the money would be paid as a form of aid or economic cooperation in exchange for permission for Japanese vessels to fish within the zone and to use Mauritanian port facilities. The Japanese delegation for negotiation was composed mainly of industry representatives.[25]

TABLE 6.—Territorial seas and exclusive fishing zones claimed by West African countries as of April 1971. Distances are in nautical miles and year of enactment is in parentheses.

Countries	Territorial sea	Outer limit of exclusive fishing zone
Morocco		12 (1967)
Spanish territories	6 (1957)	12 (1967)
Mauritania	12 (1967)	
Senegal	12 (1967)	18 (1968)
Gambia	12 (1969)	
Portuguese territories		12 (1966)
Guinea	130 (1964)	
Sierra Leone	12 (1965)	
Liberia	12	
Ivory Coast	6 (1967)	12 (1967)
Ghana	12 (1963)	[1]
Togo	12 (1964)	
Dahomey	12 (1965)	
Nigeria	12 (1967)	
Gabon	25 (1970)	
Congo (Brazzaville)	12 (1969)	
Congo (Kinshasa)	No legislation	
South Africa	6 (1963)	12 (1963)

[1] A 100-mile conservation zone (1963).
Source: FAO (1971).

Participation in International Fishery Conventions

Japan has recently joined four multilateral fishery conventions: the Northwest Atlantic fisheries convention (joined 1970), the Inter-American tropical tuna convention (joined 1970), the Atlantic tuna convention (came into force 1969), and the Southeast Atlantic fisheries convention (came into force 1971). Thus, Japan is now a member of the following fisheries commissions established under international conventions: the International Whaling Commis-

[25] The legal status of this agreement is not clear to the author. Mauritania has also concluded bilateral fishery agreements with such other nations as Greece, Italy, Spain, and the Netherlands.

sion, the North Pacific Fur Seal Commission, the International North Pacific Fisheries Commission, Japan-Soviet Fisheries Commission, the Japan-Republic of Korea Joint Fisheries Commission, the International Commission for the Northwest Atlantic Fisheries, the Inter-American Tropical Tuna Commission, the International Commission for the Conservation of Atlantic Tunas, and the International Commission for the Southeast Atlantic Fisheries now in the process of being established. As mentioned, above, Japan is a party to a large number of bilateral agreements, including some nongovernmental arrangements, with a variety of nations. Consultations have also been taking place annually between the tuna industries of the three major longline fishing nations: Japan, Taiwan, and South Korea.

FORMS OF INTERNATIONAL ARRANGEMENTS AND MEANS TO IMPLEMENT THEM

Forms of Arrangements

The official position of the Japanese government concerning high seas fishing has always been for the basic freedom of fishing and, where conservation measures are required, free competition between nations within the limitations equally applicable to all. She has always supported a narrow territorial limit; she is still not a party to the 1958 continental shelf convention, nor the 1958 convention on fishing and conservation of living resources. In practice, however, she has accepted various forms of allocation as means to accommodate the conflicting interests of the nations concerned, although she has seldom taken the initiative for making such arrangements.

The most extreme form of resource allocation is, of course, "abstention," which Japan accepted, though under unusual circumstance. In most other cases, the allocation of resources has been implemented through a combination of catch quotas, often with a system of allocating fishing grounds, and direct control on fishing effort. This applies to all salmon and crab fisheries (and now herring fishing) under the Japan-Soviet fishery agreements, the crab fishery under the Japan-United States agreement, the fisheries regulated under the Japan-Korea fishery treaty, whaling in the Antarctic as well as in the North Pacific, and many other cases. The principle of product distribution is also practiced under the fur seal treaty. In most cases, a total quota is applied to fishing in a specific high seas area and/or for a specific resource. To control fishing effort, the types and numbers of vessels allowed to operate in the area are restricted. The total quota is usually divided between operating units, such as mothership fleets or independent vessels. The available fishing grounds, too, are often allocated between different sectors of the fishery. Such usual measures as closed seasons, closed areas, size limits, gear restrictions, etc. are applied. In the case of king crab, the international tangle-net fishing grounds are divided into a number of small fishing lots which are allocated and regularly exchanged between the Soviet and Japanese fleets (see Figures 8 and 9).

Japanese responses to what she considers unilateral actions have also been rather pragmatic. For example, Japan is not a party to the continental shelf convention, while the United States and the Soviet Union are. Yet, arrangements made under the Japan-United States crab agreement and United States-Soviet crab agreement are in principle the same. Japan claims a 3-mile territorial limit, while the Soviet Union claims a 12-mile limit. But Japan has never attempted to fish within 12 miles of the Soviet coast, except around the southernmost islands of the Kurile chain. The treatment of problems arising from the establishment of an exclusive fishery zone by the United States is not substantially different between the United States-Japan fishing agreement and the United States-Soviet fishing agreement (see Figures 12-15). On a global basis, different arrangements have been made to resolve fishery problems arising from the establishment of an exclusive fishery zone. The United States-Japan fishing agreement mentioned above is on a give-and-take basis. Under the Japan-Mexico fishing agreement, Japan managed to continue tuna fishing in much of the waters concerned. In both the Japan-Australia agreement and the Japan-New Zealand agree-

ment, Japan agreed to phase out her fishing activities in the respective zones within a relatively short period of time (5 years for New Zealand and 7 years for Australia). Different forms of compensation and payment have been used, e.g., the Japan-Korea agreement, the Japan-Indonesia agreement, and the Japan-Mauritania agreement, sometimes on a large scale. Political trade offs are not unusual either. Japanese pragmatism has gone to the extent of concluding nongovernmental agreements to settle fishery problems, as seen in negotiations with the People's Republic of China and Indonesia.

In the entire history of international fisheries disputes after World War II, Japan has never contested unilateral jurisdictional claims by force. Even at the height of the Japan-Korea dispute, when a large number of Japanese vessels were being captured by Korean patrol boats, Japanese patrol boats never opened fire or tried to recapture the vessels by other means. Japan has not challenged the 200-mile territorial sea or fishing limit claimed by Latin American nations except by protests through diplomatic channels. In short, despite her rigid position regarding the freedom of fishing and limits of national jurisdiction, Japan has in practice accepted various forms of allocation, including the allocation of resources, division of catch, allocation of fishing grounds, as well as a system of revenue sharing in exchange for giving up the right to exploit a resource on the high seas (fur seal). She has done so in most cases reluctantly and after long, hard negotiations.

Means to Control Fisheries to Meet International Problems

Japan has so far found some way of settling almost every major international fishery dispute, as well as extremely complicated problems of domestic fisheries, some of which were mentioned in connection with the development of trawl fisheries in Japan. This is not an easy task, if one considers the diversity of fishing and processing activities and the enormous amount of investment in every sector of the industry. What has made it possible for the Japanese government to cope with all these conflicts from various sources is the existence of an effective, centralized system of control as briefly described in the introduction of this paper. The so-called licensing system applies to practically all offshore fisheries. Although legal authority is vested in the Minister of Agriculture and Forestry, the Fishery Agency, which is subordinate to the Ministry, has in fact full power to control all major fisheries. Thus, the central government may, and does in practically all cases, restrict the type, number, and often size of the vessels allowed to operate in a given area and/or for a given resource. Although objectives are different from case to case and change from time to time, the basic concept is to give the central government a strong means to allocate resources among different sectors of the industry to accommodate their conflicting interests. The administration of fisheries under this system is naturally subject to pressures from different groups, including large fishing companies, vessel-owner associations, and fishermen's associations, but institutional changes are made only through this centrally controlled system. The system is also used, in most cases rather effectively, to accommodate such changes as the government and industry consider necessary for meeting new international developments or resolving international fishery issues. It is, of course, debatable whether this system has in the long run facilitated the rational development of the Japanese industry, for there is no way of telling how the industry would have developed under any other system. Japan can not go back to 1946 and start developing fisheries again.

Another important factor which has contributed toward facilitating international fishery arrangements is the existence of well-organized associations representing various segments of the industry. As briefly described by Kasahara (1964), the structure of the Japanese fishing industry is one of extreme complexity. There still exist a huge number of small fishing craft, including many nonpowered vessels, while large companies operate gigantic motherships and factoryships. Between these two extremes, there are vast numbers of vessels of all kinds and sizes. The existence of the large fishing companies running most of the important distant-water fisheries deserves special attention. The following

brief description of the biggest four indicates the magnitude of large company operations (data are mostly for 1968 and do not include their subsidiary companies):

Taiyo Gyogyo Company, Ltd.

In addition to fishing, fish processing, and marketing, engaged in a wide variety of other activities.

Gross sales	$472 million.
Number of employees	10,890 including 6,880 aboard ships.
Number of vessels	486, with a combined gross tonnage of 225,000.
Major fishing activities	Whaling, the mothership salmon fishery, the mothership trawl fishery, trawl fisheries in distant waters (including the Bering Sea and northeast Pacific) and the East China Sea, overseas shrimp ventures, and others.

Nippon Suisan Company Ltd.

In addition to fishing and fish processing, a substantial interest in transport business, with four large vessels carrying oil and ore.

Gross sales	$195 million.
Number of employees	7,950 including 3,960 aboard ships.
Number of vessels	131, with a combined gross tonnage of 396,000.
Major fishing activities	Whaling, trawl fisheries in distant waters (including the Bering Sea and northeast Pacific) and the East China Sea, the mothership trawl fishery, the mothership salmon fishery, the mothership crab fishery, overseas shrimp ventures, and others.

Nichiro Gyogyo Company, Ltd.

Before the war, the company monopolized Japanese salmon fishing from the Russian territory. Now engaged in diversified activities.

Gross sales	$155 million.
Number of employees	5,800 including 3,190 aboard ships.
Number of vessels	113, with a combined gross tonnage of 98,000.
Major fishing activities	The mothership salmon fishery, the mothership crab fishery, the mothership trawl fishery, trawl fisheries in distant waters (including the Bering Sea and northeast Pacific), overseas shrimp ventures, tuna fisheries, and others.

Kyokuyo Hogei Company, Ltd.

Started as a whaling company but has since diversified its activities.

Gross sales	$85 million.
Number of employees	3,640 including 1,810 aboard ships.
Number of vessels	48, with a combined gross tonnage of 100,000.
Major fishing activities	Whaling, the mothership salmon fishery, trawl fisheries in distant waters (including the Bering Sea and northeast Pacific), overseas shrimp ventures, the tuna longline fishery, crab fishing, and others.

Among these four companies, they own practically the entire whaling business excepting minor operations by two small companies, 8 out of 11 salmon motherships,[29] roughly two-thirds of the crab fisheries in the eastern Bering Sea, three-quarters of the mothership crab fishery in west Kamchatka, some 80% of the Bering Sea mothership trawl fishery, most of the large stern trawlers operating in the North Pacific, West Africa, and other distant waters, as well as much of the shrimp ventures abroad. It means that the government can handle the industry aspects of most of the international problems concerning these fisheries by communicating with these and a few other companies (some of them subsidiaries of the big ones). The government sometimes has forced them to conduct joint operations. Thus, one of the two mothership crab fleets fishing in the eastern Bering Sea is managed jointly by four companies, the other by five companies. Representatives of these companies, particularly the first three, often participate in international negotiations.

The structure of fishery trade associations in Japan is rather complicated. The following is a brief description of some of the associations concerned with international aspects of Japanese fisheries:

[29] Salmon catcher boats are largely owned by small companies and individual vessel owners.

Japan Fishery Association (*Daisui*) generally represents the interest of larger fishing companies engaged in offshore and distant-water fisheries. It is often represented in important international fishery negotiations. It develops industry policies on international fishery problems and also deals with specific disputes. It also arranges for long-term, low-interest loans for the development of distant-water fisheries. The present chairman of the association is one of the most experienced Japanese in international fishery negotiations.

National Federation of Fishery Co-operatives (*Zengyoren*) provides nationwide representation for Japanese fishery co-operatives. Two of the main areas of activity are the procurement and distribution of duty-free diesel oil and fish marketing, but the federation is involved in international fishery negotiations from time to time.

Federation of Japan Tuna Fishery Co-operatives (*Nikkatsuren*) is the most powerful association for Japanese tuna fisheries, participated in by tuna and skipjack vessel owners through their local cooperatives,[39] and is involved in most of the international negotiations concerning tuna fisheries. Together with Zengyoren, the federation signed the Banda Sea agreement with Indonesia. The federation is making an effort to restrengthen the Japanese tuna longline fishery with substantial success. It buys in when the market is weak. It has been campaigning for increased domestic consumption of the tuna species that have been mainly exported, resulting in an appreciable increase in the consumption of canned albacore tuna. It has promoted consultations with the tuna industries of South Korea and Taiwan. It plans to institute voluntary restrictions, mainly closed seasons, on fishing for southern bluefin tuna (in effect as of October 1971). It compiles the most complete statistics of the longline fishery available in Japan.

[39] Tuna operators not eligible to cooperative membership under the Japanese fishery cooperative law, mainly companies operating large tuna boats, are organized under the Japan Tuna Fishery Association (Nikkatsukyokai). Nikkatsuren and Nikkatuskyokai always work together.

Federation of Japan Salmon Fishery Co-operatives (*Nikkeiren*) represents salmon catcher boat owners and is mainly concerned with catch quotas for the mothership salmon fishery and negotiations with mothership owners for profit sharing (formerly for selling prices). There are also associations representing such other salmon fisheries as the land-based drift-net fishery and the land-based longline fishery.

National Federation of Medium Trawlers represents bottom trawl fisheries in waters east of long 130°E, including the category called "Hokutensen" (see page 233). As the importance of "Hokutensen" increases, the association is now concerned about the condition of the pollack stocks in the northern areas (Kamchatka, North Kuriles, and Bering Sea) on which the entire fishery is based.

Japan Trawler Fishery Association represents trawl fisheries (largely by pair trawlers) in the China Sea. They have been concerned with problems with South Korea and the People's Republic of China.

Japan Deep-sea Trawlers Association represents companies operating large distant-water trawlers, and has been active in negotiations with Mauritania (Chairman of the association served as the Japanese chief delegate). It has made arrangements for exploratory trawl fishing for new grounds, and has engaged in planning the production of pollack minced meat ("surimi").

Except the first two mentioned in the above list, these associations represent the interests of specific fisheries and provide a convenient means of communication between the government and industry in connection with international negotiations involving such fisheries.

IMPACT OF JAPANESE FISHING

The expansion of the Japanese and Soviet fisheries has caused more international fishery problems than any other single factor. To be fair, some credit should be given to these two nations for their contribution towards development of new fishery resources all over the world. Japan and the Soviet Union, for example, have developed new resources in the Bering Sea and

adjacent areas which now support an annual combined yield of perhaps 3 million metric tons and which would have remained unexploited or grossly underexploited without their effort. Japan has developed the tuna resources of the world ocean exploitable by longline. Again along with the Soviet Union, Japan initiated large-scale exploitation of groundfish resources along the west coast of Africa. The Soviet Union has been most active in developing new resources in the northwest Atlantic area. Japan has developed other resources, though not as great as those mentioned above, in various parts of the world.

On the international scene, however, Japan has seldom been given credit for her contribution towards resource development, for the impact of Japanese distant-waters fisheries on the resources in international waters, some of which are also utilized by coastal states, was such that many nations look upon Japanese fishing, along with Soviet fishing, as one of the major factors responsible for the depletion of fishery resources on a global basis. There are many obvious cases in which Japan should be blamed for overexploitation of the resources that were either utilized by other states at the same time or were considered important potential resources for them. Japan and the Soviet Union are largely responsible for the present state of the Antarctic whale stocks; Japan obviously overexploited many of the important stocks in the East China Sea; she overfished the yellowfin sole stock in the eastern Bering Sea, which was also an important resource for the Soviet Union; the impact of offshore salmon fishing on the Soviet salmon stocks is apparent, although no critical assessment has been carried out; many of the crab stocks in the Bering Sea and Kamchatka have been overexploited to varying degrees; some of the stocks of porgies (sparids) in West Africa have been overfished by the trawl fisheries of Japan and some other nations.

In other instances, Japanese fishing has not had any substantial effect on the fisheries of the coastal states concerned, as is the case with the pollack fishery in the Bering Sea, much of the tuna and skipjack fishing, deepwater trawling, fishing for cuttlefish and octopus in northwest Africa, herring fishing in the eastern Bering Sea, squid fishing off New York, etc. But even in those cases, the way new resources have been developed by the Japanese looks frightening to many other nations. A new resource may be exploited to a maximum level within several years, sometimes in 2 or 3 years. Emphasis shifts from one resource to another, or from area to area. The way Japanese trawl fisheries in the Bering Sea and adjacent areas are being expanded mainly based on one species, pollack, makes biologists wonder how long the resource can support the fisheries and what would happen if the pollack stock collapsed suddenly.

This new pattern of fishing, characterized by concentration of effort through large fleet operations and shift of emphasis from one resource to another, may not necessarily be a bad strategy from the point of view of maintaining the total production and the profitability of the industry. But it is not acceptable to many other nations because it is contradictory to the established principles of management based on the concept of maximum sustainable yield and, more important, because such a pattern of fishing can be adopted only by nations having well-organized distant-water fisheries. If a nation is unable to participate in the utilization of a resource for technological or economic reasons, she would rather keep it undeveloped than see some other nation exploit it.

There is little doubt that the development of Japanese and Soviet distant-water fisheries has had very appreciable effects on the international fishery regimes. The impact of these fisheries, whether real or imaginary, has been one of the major factors motivating unilateral jurisdictional claims by coastal states. This applies, for example, to actions taken by the United States, Canada, South Korea, some of the Latin American nations, many of the West African states, and even some of the Southeast Asian nations. Even the Soviet Union has taken unilateral actions to protect its fisheries against Japanese high seas activities. In addition to these events, the expansion of Japanese and Soviet fisheries has been at least partially responsible for a worldwide trend for coastal states to justify various forms of jurisdictional control as effective means to deal with international fishery prob-

lems. Whether or not the Law of the Sea Conference can produce a general agreement on this matter, some principle to the above effect is likely to emerge as a consensus of the majority. Exactly to what extent the development of distant-water fisheries has contributed to this general trend is difficult to assess. It should also be pointed out that some of the European nations, particularly the east European, have followed the example of Soviet fishery development, though on a smaller scale, and have accelerated the trend for extension of coastal jurisdiction.

FUTURE PROBLEMS

CHANGES IN REGIMES FOR FISHERIES

The purpose of this section is to make predictions, based on past performance, on how the Japanese government and industry might respond to possible changes in international regimes for marine living resources.

First, a brief analysis of the changes in international regimes that are most likely to take place appears appropriate (Kasahara, in press). The first preparatory meeting of the Law of the Sea Conference (scheduled for 1973), held in March 1971, made it clear that fishery problems were among the most controversial issues concerning uses of the ocean. One of the reasons for this is the fact that fisheries are important to many of the developing countries, which comprise the overwhelming majority of United Nations membership. Another factor, which may be more important, is the very nature of fishery problems. It is perhaps useful to note how well some of the major uses of the sea have been served by the existing regimes based largely on the traditional concept of free access. These include transportation, which is the most important use of the sea, communication, scientific research, and recreation. Even the exploitation of mineral resources has not caused insolvable international conflicts. Although developing nations might look upon such freedoms as inequitable because of their limited participation, little real damage has been done in those aspects of use of the sea. The major exceptions to this general notion are fishing and pollution. Except for pollution from sea accidents, most of marine pollution originates in areas within the limits of national jurisdiction rather than beyond. This leaves fishing as the most controversial issue.

Free access to fishing on the high seas may have served for increasing food production from the sea, but it has resulted in numerous international conflicts and necessitated almost continuous negotiations between nations all over the world. Most of the actions taken to extend national jurisdiction in one form or another have been motivated by a desire to control use of living resources. Fishery interests have also created such new concepts as an exclusive fishery zone, preferential rights of coastal states, as well as the allocation of resources in international waters.

Judging from the nature of recent fishery conflicts and discussions in the United Nations system, one of the predominant trends will obviously be further extension of coastal jurisdiction over the exploitation of living resources. Such a trend will continue regardless of the outcome of the Law of the Sea Conference. Extension of coastal jurisdiction might take the form of broader territorial zones, or preferential rights of coastal states. National claims might also be expanded through a new definition of living resources subject to the existing continental shelf convention and/or a new sea-bed treaty now under consideration. It is also possible that some nations might translate the new regime for sea-bed resources into a regime for the control of living resources in superjacent waters.

There is no question that most of the developed nations would prefer a relatively narrow territorial sea as a general rule from the point of view of minimizing potential hazards to important nonextractive uses of the sea, particularly shipping and navigation. The probability of coastal states taking unilateral actions to restrict the right of passage for nonmilitary purposes is rather remote, since practically all nations are beneficiaries of this right, and such actions would result in retaliatory measures of various kinds. Nevertheless, under certain circumstances, some nations might possibly take such actions for economic gains. However small

the probability might be, the stake is big enough for a substantial number of nations to try to block a proposal for a territorial sea wider than 12 miles, or, failing this, to refuse to sign any treaty containing such a provision. Thus, chances are slim for an *effective* global treaty specifying a territorial sea broader than 12 miles to come out of the proposed 1973 conference. This will not, of course, prevent some nations from extending their territorial seas through unilateral claims. If any effective global agreement on fishery matters should come out of this conference, however, it would be based on the principle of separating out the question of jurisdiction over fisheries from the total package of national jurisdictions comprising sovereignty.

The conference may not result in an overall agreement on fishery issues, but it is quite likely that there will be a general recognition of special rights of coastal states in terms of exclusive fishery jurisdiction or other forms of preferential allocation of resources. Such a principle will be supported not only by developing nations but also many of the developed nations.

One way of protecting fishery interests of coastal states beyond the territorial sea would be the recognition of exclusive fishery jurisdiction within a certain zone, perhaps defined in terms of a fixed distance and/or a depth. It would be up to the particular coastal state whether it chooses to allow foreign fishermen to fish within the zone under conditions set by the coastal state. Some coastal states might prefer to allow foreign fishing for the resources that are not utilized or grossly underexploited by their own fishermen, probably charging foreign vessels a substantial fee. Arrangements might also be made for such resources to be developed from coastal bases as a condition for allowing foreign fishing.

Another way of protecting the interests of coastal states would be for coastal fisheries to be given preferential rights (including a right to adopt and implement conservation measures which would be binding on foreign vessels) to all resources within a certain zone beyond the territorial limit. This would involve problems of determining what portions of such resources or catches therefrom should be allocated to the coastal fisheries concerned, including the question of whether the coastal state should have a right to control the exploitation of the resources that are not used by them to any substantial degree. Under this principle, the formula to be adopted would perhaps vary from case to case. Preferential fishing rights might also be applied to specific resources important to the coastal states without establishing a fixed zone. This would involve such additional questions as the determination of major areas of distribution of the resources concerned, and the effect of foreign fishing for other resources on the particular resources in the same area.

Among the three alternatives mentioned above, more nations might favor the first to ensure a greater degree of control and simplicity of implementation. The main question in this case would be how the zone should be defined. Some of the nations supporting this idea may still be thinking in terms of a distance of 12 nautical miles from the shore for their exclusive fishery zone, with a narrower territorial sea. Some others are apparently considering varying distances to meet the specific situations. A substantial number of nations seem to favor much greater distance, up to 200 miles, and/or to the outer edge of the continental shelf.

A small number of nations might prefer preferential fishing rights for specific resources that are important to their coastal fisheries. This would be a rather complex concept and a variety of problems would arise from its implementation. Many different formulae could be considered. The existing arrangement for yellowfin tuna in the eastern tropical Pacific may fall in this general category in that allowance is made, within the total catch limit, for vessels of smaller carrying capacities. Various bilateral fishery agreements between the United States and nations operating distant-water fisheries off her coast also include provisions for reducing the adverse effects, on coastal fisheries, of foreign fishing on the high seas. The treatment of anadromous fishes, particularly salmon, and marine mammals returning to land for breeding might also be considered a special case in this general category. Different formulae are in practice to handle such a case. For North American salmon, the absten-

tion principle prohibits fishing by Japan in the eastern half of the North Pacific and Bering Sea. Catches of Asian salmon, on the other hand, have been shared by the Soviet Union and Japan. A system of product distribution has been applied to the harvesting of North Pacific fur seals.

Along with the general trend of extension of coastal jurisdiction, there will also be a continuing trend for more bilateral and multilateral fishery agreements between the nations directly concerned. International agreements solely for conservation, that is, for the purpose of maximizing the total catch, have become less and less attractive to most nations, and emphasis has shifted to arrangements combining systems of allocation with conservation measures. The question of national quotas, particularly for the heavily exploited stocks, will undoubtedly become one of the most critical issues of fishery negotiations in the future. National quota systems are now being discussed even by some of the international commissions which originally did not envisage them, as is the case with the Inter-American Tropical Tuna Commission or the International Commission for the Northwest Atlantic Fisheries. There is no established set of principles as to how the allowable total catch from a stock or stocks should be divided among the nations exploiting such a stock or stocks in waters beyond the limits of national jurisdiction, nor as to what allowance should be made for new entry.

It is not very likely that the Law of the Sea Conference would come up with any specific formula to divide the limited catch. It is possible, however, that discussions at the conference might result in the general acceptance of the establishment of national quotas as a principle of international regulation of fisheries without spelling out details to implement it (such details would be left to bilateral or multilateral agreements between the countries concerned).

In any case, changes likely to take place in the regimes for regulation of fisheries, with a predominant trend for extension of national jurisdiction by coastal states, may result in more international negotiations rather than less. In many parts of the world, such as Southeast Asia, the Gulf of Mexico and the Caribbean, the South Pacific Islands, West Africa, or even in much of Europe, the question of determining the boundaries between areas of national jurisdiction of neighboring states would become enormously complicated and, in some cases, might never be solved. Negotiations for the handling of historical rights of noncoastal states, as well as of neighboring coastal states, in the extended area of national jurisdiction of each state, would also take time. In many regions, regional arrangements of various kinds would have to be negotiated among neighboring coastal states to accommodate each other's fishing activity. Without such arrangements, the development of the fisheries of coastal states would be hampered greatly, and the proper management of stocks of fish crossing several national boundaries would become impossible. In the present political environment, I doubt that the countries concerned could agree to a single regional convention for each region. In most areas, a complex network of bilateral and semiregional agreements would develop. The enforcement of these arrangements would also be difficult and costly.

POSSIBLE RESPONSE

The question of how Japan might respond to likely changes in international regimes for fisheries is, to a substantial degree, answered by what she has done in the past in response to various claims by other nations (see section on International Arrangements). If the Law of the Sea Conference results in a global convention providing for extensive coastal jurisdiction or broad preferential rights of coastal states, it is unlikely that Japan will be a party to such a convention. She would then regard actions taken by member states of the convention as unilateral. In the past, Japan has responded to unilateral actions in a variety of ways. When she did not have much vested interest in the zone claimed and the nation claiming the zone was not prepared for negotiating the issue, Japan voluntarily refrained from fishing in the zone while refusing to recognize the claim. When her vested interest was very substantial, Japan entered into negotiations with the country concerned. In some cases, such as the Japan-South

Korea controversy, the Japanese government did not stop fishing vessels of its nationals from entering the claimed zone, resulting in the seizure of many vessels. In most cases, however, practical arrangements of various kinds were agreed upon, sometimes after long negotiations, as described before. Japan has not challenged any fishery claim by force, and, except for the Japan-South Korea and Japan-Soviet controversies, no real diplomatic crisis has developed from fishery issues.

The future trend in this respect will be about the same. Japan would do her best to protect her fishery interest against unilateral claims with whatever trade offs available to her, both within and outside the purview of fisheries, but would still seek a pragmatic solution to settle the issue. If Japan has no vested interest in the area claimed, she might voluntarily refrain from entering the zone for fishing while officially refusing to recognize the claim. The same would perhaps apply to Japan's reaction to claims based on the concept of preferential rights of coastal states.

Such concepts as the allocation of resources, the division of catches therefrom, or the distribution of benefits, have already been applied extensively to fishery arrangements involving Japan. Although Japan would not recognize these as internationally accepted legal concepts, she would not object to practical arrangements which would have the same effects. The application of a limited entry system has never been a problem to Japan because of the very nature of her domestic regulations, as outlined in the introduction of this paper. In most of the bilateral agreements she has made so far, the number (and in many cases the size as well) of the vessels to operate in a designated area is limited.

Any substantial change in the definition of shelf resources to include more living resources currently exploited would not be recognized by Japan officially. The main reason for Japan not to sign the 1958 continental shelf convention was the inclusion of living resources. The pattern of bilateral negotiations for problems that might arise from this source would be about the same as that for problems from extended fishery jurisdiction. She would do her best to protect the vested interest of her fishing industry.

The possibility of general recognition of a special right to anadromous species, particularly salmon, would be a matter of great concern to Japan, as high seas salmon fishing is still one of the most important sectors of the Japanese fishing industry. During the Law of the Sea Conference, the establishment of a special right to anadromous species may be proposed by some nations as one of the principles of international regulation of fisheries. This might receive rather broad support, not only because of problems of Pacific salmon but also in view of recent developments in offshore salmon fishing in the Atlantic. Again, Japan would not join a convention including such a provision. But if the United States, Canada, and the Soviet Union should claim, on the basis of such a convention, a special right to anadromous species for the main purpose of eventually eliminating high seas salmon fishing, Japan would be in a difficult position to protect her interest in salmon fishing.

The idea of establishing a world agency for regulating all high seas fisheries has been talked about by idealistic people, but by now it is widely recognized that this is not feasible, nor even desirable. We can pretty well eliminate this possibility from our consideration of fishery problems in the foreseeable future.

In short, it is unlikely that Japan could take any definite course of action to cope with an increasing number of international problems she is going to face. She must be prepared for more and harder negotiations to find a practical solution to each of the problems. In the North Pacific, Japan will have to keep negotiating with the Soviet Union for salmon, crabs, and herring, and probably for some of the groundfishes in the future. Negotiations have become increasingly difficult as additional regulatory measures have been proposed by the Soviet Union every year. As the U.S. king crab fishery in the Bering Sea is expanding with the Japanese quota being reduced, the future of the Bering Sea king crab fishery also looks bad. Continuous pressure will come from the United States and Canada to provide their coastal fisheries with a

greater amount of protection against Japanese fishing for groundfishes and shrimp. Pollack, the main species for the trawl fisheries in the Bering Sea and Kamchatka waters, might become a serious international problem in the near future. Japanese fishing pressure is still mounting; the Soviet catch is increasing; South Korea is building a number of stern trawlers in Japan with a view to rapidly increasing her participation in pollack fishing. The Japanese trawl fishery along the west coast of Africa will face further international problems as more African nations take measures to extend fishery jurisdiction. Most of the bilateral agreements Japan has concluded in recent years are of short duration, and it may be difficult to continue these on the same terms.

The Japanese tuna industry might still be able to compete with the Taiwanese and Korean fisheries by taking advantage of rapidly expanding domestic markets, but a substantial increase in the catch of the longline fishery is not likely. Major efforts are being made to develop a purse-seine fishery similar to that of the United States and to increase the production of skipjack, which is at present an underexploited resource; but international regulations will gradually be applied to many of the tuna fisheries. In the eastern tropical Pacific, the present pattern of tuna fishing is likely to lead to a system of national quotas. Tuna fisheries in the Atlantic will also be subject to some international regulatory system in the future. Eventually there might be a regime of worldwide regulation covering all major tuna fisheries. Trawl fishing in the Northwest Atlantic will also be subject to further restrictions through bilateral and multilateral arrangements. Whaling both in the Antarctic and the North Pacific will have to be further curtailed.

International fishery problems faced by the Soviet Union are not too different from those confronting Japan, except in the Northwest Pacific where the Soviet Union finds herself in the position of a coastal nation seeking protection against Japanese fisheries. It is interesting to note that their responses to unilateral claims have not been too different from those of Japan.

FUTURE OF THE INDUSTRY

The phenomenal growth of the Japanese economy has greatly increased demand for high-quality foods, particularly animal protein products. The per capita consumption of animal protein increased by 19% in the 5-fiscal year period of 1963-68. About 58% of the animal protein intake is still from seafoods, including whale meat. During the same period, the per capita expenditure for fishery products increased by 10% per annum in cities and 13.2% per annum in rural areas (Anonymous, 1969). Markets have also developed for a greater variety of fishery products. Imbalance between demand and supply has been increasing constantly, pushing up prices sharply. Pressure for increased fish supply is still quite strong in Japan.

Domestic Production

What alternatives are available for Japan to meet this problem? First, let us examine the possibilities of increasing the domestic supply of fish. Figure 16 indicates the trend for production by four sectors of the Japanese marine fishing industry. Divisions between the sectors, except aquaculture, are somewhat arbitrary.

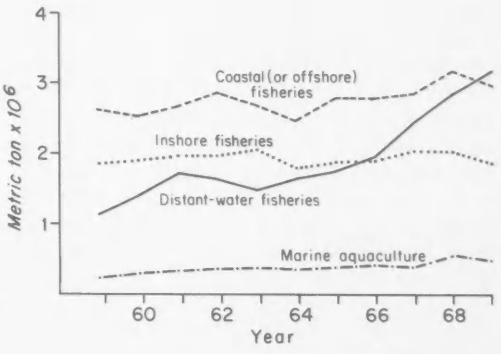

FIGURE 16.—Production of four sectors of the Japanese fishing industry 1959-69 (from Ministry of Agriculture and Forestry, 1971). Division between inshore fisheries and coastal (or offshore) fisheries is somewhat arbitrary. Distant-water fisheries include trawl fisheries in the China Sea.

The total production of inshore fisheries has stayed about the same for the last 10 years, a little less than 2 million metric tons. The total catch of coastal fisheries (called "offshore fisheries" in Japan) has shown a substantial increase, but has been influenced by fluctuations of a few pelagic species. (Mackerels and common squid, for example, account for a sharp increase in 1968.) Distant-water fisheries have contributed greatly to a general increase in production during the last 10 years, but pollack account for the largest portion of the growth. In fact, many of the other distant-water fisheries have shown a decline in the most recent years. Pollack are largely processed into minced meat and fish meal. The domestic production of fish meal has also increased rapidly during the same period.[31] Fish meal is manufactured on factoryships, now mainly from pollack, as well as on land, from mackerel, some other coastal pelagic species, and pollack.

Inshore fisheries.—This sector consists of fishing by small vessels (particularly draggers), coastal traps, beach seines, and other miscellaneous methods including collection of bivalves and seaweeds. Virtually all stocks in inshore waters are exploited very intensively, and no increase in production would be possible by further intensifying fishing efforts. Theoretically it might be possible to improve the fisheries in this category by introducing better management measures, but it would create enormous social and economic problems. The fisheries are tightly controlled by the long-established fishing right system largely operating through cooperatives.

This sector of the industry has always presented difficult social problems due to low productivity (efficient fishing methods are usually outlawed) and overemployment. Unlike farmers around urban areas, who have become rich by selling their land for industrial or residential use, these fishermen have nothing to cash in. Social problems of small fishing communities along the Japanese coast will only be solved gradually by young people being absorbed in manufacturing industries. The industrialization and urbanization of the coastal zone is becoming a real threat to inshore fisheries, particularly those in bays and estuaries. Inshore fisheries are still important in Japan for providing consumers with fresh, high-priced seafoods, but the possibility of increasing their total production has to be written off.

Coastal (or offshore) fisheries.—This category includes all fisheries carried out by medium-sized vessels. They include Danish seining, pair trawling, purse seining, saury fishing, tuna longlining by smaller vessels, salmon fishing by smaller vessels, skipjack fishing by smaller vessels, pole-and-line fishing for mackerel, squid fishing, and others. Some of these fisheries are conducted in fairly distant waters, for example, tuna and skipjack fishing or offshore saury fishing. Except in the last 2 years, this sector has produced the greatest proportion of the total catch of the entire Japanese fishing industry.

While the catches of groundfishes around the Japanese islands have been relatively stable, under very strong fishing pressure, the catches of coastal pelagic species have fluctuated greatly as outlined in Other Fisheries, pages 243 to 245. All of these species have been exploited very intensively. Although Japanese scientists do not agree on the causes of the declining catches of some of these species, particularly sardines (*Sardinops*) and saury, overfishing is a strong possibility. The causes of a rapid increase in jack mackerel during the late 1950's and early 1960's and in mackerels (mainly *Scomber japonicus*) in the late 1960's are also unknown. This sector of the industry will continue to face large fluctuations in the catches of major pelagic species, but a long-term increase of the total catch is unlikely. The total production of major coastal pelagic species, including mackerels, jack mackerel, anchovy, saury, sardines (now very insignificant), and squids during 1956-69 is shown in Figure 17. (The figure includes catches by inshore fisheries.) The introduction of better methods of resource manage-

[31] As in most other industrialized countries, demand for fish meal as animal feeds has risen sharply and has been met mainly by domestic supply and partly by imports. Domestic producers have been protected by an import quota.

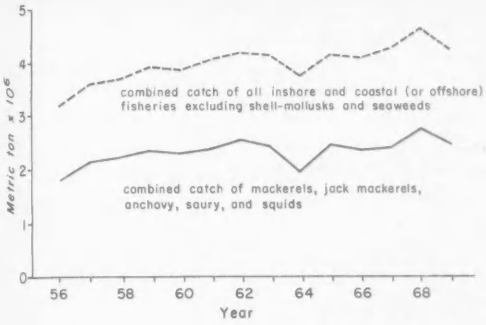
Metric ton x 10^6
combined catch of all inshore and coastal (or offshore) fisheries excluding shell-mollusks and seaweeds
combined catch of mackerels, jack mackerels, anchovy, saury, and squids
Year

FIGURE 17.—Combined catch of mackerels, jack mackerels (including *Decapterus*), anchovy, saury, and squids, 1956-69 (from Ministry of Agriculture and Forestry, 1971).

ment does not appear practical at the moment, because of the complexity of regulations under the licensing system and the lack of understanding of the causes of sharp decreases or rapid increases in the abundance and catch of coastal pelagic species.

In the long run, however, this is one area in which substantial improvements in efficiency, and possibly in total production, might be possible largely by reducing fishing effort. This applies to both demersal species and coastal pelagic species. This would require major political decisions, with great social and economic implications. Such a process would take many years in any case.

Distant-water fisheries.—Although the total production of distant-water fisheries has increased very sharply, the catches of many fisheries in this category have actually been on the decline in recent years, due to international regulation, decreases in abundance of many stocks, and increasing competition with other countries. The total catch of the mothership salmon fishery in the Northwest Pacific has decreased from 71,000 metric tons to 40,000 tons in the last 10 years. (That of the land-based salmon gill-net fishery has decreased from 85,000 tons to 55,000 tons in the same period.) The king crab catch by the mothership crab fishery has declined from 15,000 tons in 1964 to a little over 9,000 tons in 1969. The loss has been compensated by a sudden increase in the tanner crab catch in the last 3 years. The combined catch of all home-based tuna longliners has declined from the peak of 386,000 tons (including nontuna species, such as billfishes, swordfish, and sharks) in 1962 to 317,000 tons in 1969, and that of foreign-based operations (in the South Pacific, Indian Ocean, and Atlantic) from 118,000 tons in 1965 to only 28,000 tons in 1970. The catch of the mothership tuna fishery (with deck-loaded catchers) has also decreased, from 68,000 tons in 1964 to 38,000 tons in 1969. The long-established pair-trawl fishery in the China Seas has been at about the same level for the last 10 years, with a slight decline in the most recent years. The total catch of the trawl fisheries in the Atlantic increased rapidly until 1967 and has stayed at about the same level since then.

The sharp increase in the total catch of distant-water fisheries, shown in Figure 16, is accounted for mainly by the expansion of the trawl fisheries in the northern North Pacific. The catch of the mothership trawl fishery has increased from 169,000 metric tons in 1959 to 862,000 tons in 1969. The catch of independent trawlers increased from 2,000 tons to 373,000 tons in the same period, and that of "Hokutensen" from nothing to 768,000 tons. The mothership trawl fishery in the Bering Sea first depended mainly on yellowfin sole, but emphasis shifted to other species, particularly pollack, when the flounder stock in the eastern Bering Sea declined sharply.

Since the introduction of minced meat ("surimi"), the proportions of pollack in the catches of these trawl fisheries have jumped up. As of 1969, 678,000 tons out of 862,000 tons caught by the mothership trawl fishery were pollack. Corresponding figures for independent trawlers were 200,000 tons out of 373,000 tons (they take substantial quantities of ocean perch in the Aleutian and the Gulf of Alaska). Those for Hokutensen were 670,000 tons out of 768,000 tons. The total catch of pollack by distant-water fisheries has risen from 33,000 tons in 1959 to 1.55 million tons in 1969. The corresponding figures for the coastal fisheries are 343,000 tons and

396,000 tons. The pollack catch is still increasing; several 5,000-ton class vessels, newly built, are coming into operation. The recovery rate of minced meat from pollack is relatively small, probably between 20 and 25%, and the remainder goes to fish meal and oil. But the price of pollack surimi, used for making fish cakes ("kamaboko," "chikuwa") and other products, is so high that it makes all the difference in the profitability of the trawl fisheries in the northern areas. The price of fish meal is also high, around $200 per ton. Although imports of fish meal are scheduled to be liberalized this year, a high import duty will be levied when imports exceed a certain quantity still to be fixed.

Search for new distant-water fishing grounds continues, and there have been some developments in this area, such as deepwater trawling around the mid-Pacific islands, squid fishing off the Atlantic coast of the United States, trawling in the Gulf of Aden for sea breams and cuttlefish, or fishing for barracouta (*Leionura*) off New Zealand. Although further effort will be made in this direction, most of the abundant resources of traditional species are likely to be in areas relatively close to the coasts of foreign countries. Thus, uncertainties about the future regimes for fisheries are a discouraging factor. Trawling in waters deeper than 500 m, expansion of skipjack fishing, particularly in the tropical Pacific, and the development of cephalopod resources in various parts of the world, are good possibilities. In general, however, prospects for further expansion of Japanese distant-waters fisheries to harvest conventional species by known methods do not appear bright.

Aquaculture.—As shown in Figure 16, the yield of marine aquaculture has been increasing steadily. Since aquaculture includes a variety of things, we must examine a breakdown of the total yield, which is shown in Table 7. Out of the total of 473,000 metric tons produced by marine aquaculture in 1969, 245,000 tons were oysters *with shell.* The equivalent figure for oyster meat is estimated at 37,000 tons. Next comes laver ("nori," *Porphyra*) at 134,000 tons; "wakame" (also seaweed, *Undaria*) accounts for 60,000 tons; the remainder, 34,000 tons, consists of cultured fishes and various invertebrates. Thus, in terms of animal protein products, 37,000 tons of oyster meat and 34,000 tons of fish and other animals are all that is produced by marine aquaculture. Aquaculture for oysters and laver can still be expanded. It is facing, however, mounting problems arising from the industrialization of the coastal zone, particularly pollution and land reclamation. The main fish species for marine aquaculture in Japan is yellowtail (*Seriola*), others being quite insignificant in quantity. Shrimp culture in Japan is advertised all over the world, but actual production in 1969 was only 300 tons.

TABLE 7.—Aquaculture production, excluding pearl culture, in 1969.

Aquaculture	Live weight
	metric tons
Marine:	
Laver	134,320
Wakame	59,821
Oysters (meat weight)	(36,988)
Oysters (shell weight equivalent)	245,458
Yellowtail	32,613
Puffer	52
Other fishes	481
Octopus	50
Shrimp (*Penaeus japonicus*)	295
Spiny lobster	2
Swimming crab	1
Other aquatic animals	102
Total	473,195
Freshwater:	
Trouts	10,254
Carps	13,971
Crucian carp	1,776
Eels	23,276
Other fishes	2,762
Total	52,039

Source: Ministry of Agriculture and Forestry (Japan) (1971).

Freshwater aquaculture produces a substantial amount of fish: 23,000 tons of eels, 14,000 tons of carp, and 10,000 tons of trouts in 1969. The yields of these species have increased very substantially in the last 10 years, but the total production of freshwater fish culture is still a little over 50,000 tons. All aquaculture for fishes and crustaceans, in both seawater and fresh water, is carried out by intensive feeding. In most cases, fishes (largely coastal pelagic species) and fish meal are the main animal protein components of feeds. On a round-weight basis, the amount of feed fish required for yellowtail and eel culture is perhaps 7 to 8 times the amount

of fish produced. It is estimated that the consumption of fish meal for culturing eels and trouts alone might reach 100,000 tons in 1971 (the equivalent of half a million tons in live weight). Fish culture in Japan is obviously a means to produce high-priced products and not to increase the total supply of animal protein from the sea. While demand for cultured fishes remains very strong, the aquaculture of the two most important forms, eels and yellowtail, has a serious weakness. Their young have to be collected from natural waters. The domestic supply of young eels is declining, due at least partly to pollution in estuarine waters, and a substantial quantity is now being imported. The price of elvers is reported to be nearly $38 a pound.

The above review of prospects for expansion of each of the main sectors of the fishing industry indicates that it will become increasingly difficult for the domestic supply of fish to meet the evergrowing demand. In the long run, better management of coastal fisheries may result in a substantial increase in the total harvest, but this is a painstaking and time-consuming process. Further exploitation of resources in distant waters may result in some increase, but the scarcity of readily exploitable resources and uncertainties about international problems are major obstacles. Expansion of aquaculture is possible, but it would have the effect of further reducing the total amount of food fish available as long as fish and fish meal are used as major components of feeds.

Exploitation of unconventional species.—Man will have to make serious attempts to exploit unconventional species in order to sustain a reasonably high rate of growth in fishery production. What is meant by unconventional species is those forms which occur in great abundance in wide areas of the ocean and which are difficult to harvest and market economically with known methods. The utilization of these resources is in a way a continuation of the recent trend for exploiting a greater variety of species. It appears, however, that some technological breakthroughs would be required to begin large-scale commercial exploitation of such forms as the Antarctic krill (*Euphausia superba*) and other larger zooplankton, red crab (*Pleuroncodes*), lanternfishes (myctophids), gonostomatids, deepsea smelts (bathylagids), etc. Large concentrations of lanternfishes have been found in most parts of the ocean. An enormous biomass of bristlemouth (*Cyclothone*) occurs in the tropical Pacific. The abundance of deepsea smelts in the California Current system is well known. Particularly interesting in this respect is the existence of extensive offshore areas of upwelling associated with the equatorial current systems (Cushing, 1969).

The Soviet Union has been making effort to utilize *Euphausia superba* through experimental fishing and processing, with limited success. Japan has a modest program to explore the possibility of using larger zooplankton and progress has been reported in making some products out of euphausiids. Both nations still have a long way to go in this area. Furthermore, fish meal and other products into which these forms might be processed are unlikely to substitute for highly demanded conventional species although they might increase the supply of feeds.

International Business Arrangements

One might think that Japan must have been very active in developing joint ventures and other forms of international arrangements to carry out fishing from the coastal states near the fishing grounds. For a variety of reasons, her activities in this general category have been limited to a few things, such as use of facilities for transshipment of tuna caught by longliners, joint ventures for shrimping, and more recently joint ventures for skipjack live-bait fishing. Japanese trawlers operating in West Africa have been selling some of the catches locally and a few vessels still operate under contracts with local companies.

There are a variety of reasons for the lack of major developments in this general area. In many cases, the local governments establish various requirements as conditions for land-based foreign operations, such as investment in shore facilities or nationalization of equipment and crews. They may be reluctant to make such concessions as tax-free imports of equipment

and supplies. Political instability may make investments extremely risky. As long as the same types of fishing can be carried out by their own boats without heavy local investments, the Japanese companies would prefer not to make complicated arrangements with local firms or governments, except for use of local facilities for transshipment.

A major exception in this regard is shrimping, for most of the rich shrimp grounds are even now within the limits of national jurisdiction of coastal states. The existence of excellent international markets for shrimp makes joint ventures attractive even under difficult local conditions. A number of Japanese companies have recently begun shrimping in the rich grounds of Indonesia, including West Irian. Live-bait fishing for skipjack in areas far from the home islands is another type of operation which has to be carried out from local bases. Joint ventures with Australia (from New Guinea) and Indonesia (from West Irian) are now developing. Transshipping of frozen tuna through foreign bases is an essential part of the worldwide longline fisheries. Trawl fishing vessels in the Atlantic use Las Palmas and Cape Town as their main bases of operation.

The situation is changing, as more and more nations are inclined to extend their national jurisdiction. Already, use of local facilities is a condition for tuna fishing in the Banda Sea under the Japan-Indonesia agreement, and the delivery of catches by some vessels to local facilities is a condition for fishing under the Japan-Mauritania agreement. Payments are involved in both cases.

As far as the industry is concerned, fishing with payments, without further local involvement, might be preferable to other arrangements in many cases. The industry could include the amounts paid (if they are reasonable) in the costs of products and charge them to consumers. The main problem here is the official position of the Japanese government concerning the territorial sea and fishing jurisdiction. Payments could still be made under other names than licensing fees; for example, as payments for use of local facilities. The government of the coastal states, on the other hand, might not agree to such an arrangement which could weaken their positions on jurisdiction. Since there are already precedents of this sort (Indonesia, Mauritania, and Australia), however, this approach may be used more widely in the future.

Another direction in which the industry might move is more direct investments in the prosperous foreign fishing and processing industries. The United States has gone far ahead of Japan in this area. Japan now has a small interest in the Peruvian fish meal industry. I do not quite understand why some of the large Japanese trade companies, which handle various fishery products, have not vigorously explored possibilities of direct investment in foreign fishing industries. The government used to discourage involvement of Japanese firms in foreign fishing ventures for fear of increasing competition with Japanese fisheries. But the main reason may now be that there are not many fisheries in foreign countries which offer long-term returns comparable to those expected from other industries, perhaps with the exception of fish meal and shrimp operations in some areas.

Imports

As shown in Figure 18, there has been a marked increase in imports of fishery products in the last 10 years, while exports have generally leveled off. For many years, however, the Japanese government has imposed rather strict restrictions on imports of fishery products, mainly based on two considerations: the balance of payment and the competition with domestic products. With the foreign exchange surplus increasing at an almost embarrassing rate, the balance of payment is no longer a problem. On the contrary, pressure is mounting for the government to facilitate importation of many items including food in general. Internationally, Japan has been urged by both developed nations (including the United States) and developing nations to relax trade restrictions. Also, the government must explore all means to accelerate foreign currency spending to reduce the rate of increase in the surplus and slow down inflation. Increased imports of food items are generally considered desirable from this point of view.

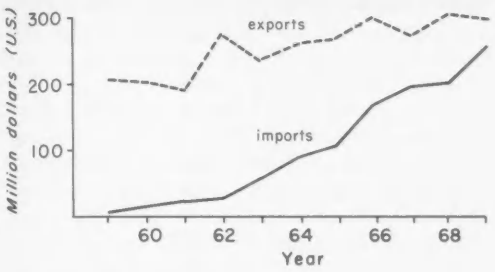

FIGURE 18.—Imports and exports of fishery products, 1959-69 (from Suisan-sha, 1970). Pearls are excluded. Figures for 1969 are estimates. ¥360 per dollar.

The liberalization of the import of fishery products began only in 1960, and a major change took place in 1961 when a number of fresh and frozen fishes and shellfishes were removed from the list of restricted items. Many items, however, still remain on the list mainly to protect the interests of inshore and coastal fisheries. The Japanese system of control of fishery imports is quite complicated. An attempt is made below to describe it briefly (from Suisan-sha, 1970).

As of 1970, all imports of fishery products fell under two categories: those which are not subject to quotas (Automatic Approval System, abbreviated AA) and those which are subject to quotas (Import Quota System, IQ). Among important AA items are a number of fresh or frozen fishes and shellfishes, including shrimp, tunas (including skipjack), swordfish, salmon, porgies, etc.; most of the canned fishes; and whale meat. Among important IQ items are a variety of fresh and frozen fishes, including herring, cod and pollack, yellowtail, mackerels, sardines and anchovy, jack mackerels, saury, cod (or pollack) roe, herring roe, as well as salted, dried, or smoked products of these species; laver and kelps; fish meal and whale meal, as well as mixed feeds or fish solubles; and fresh, frozen, or dried squid and cuttlefish. As Japan is now a party to IMF (International Monetary Fund) Article 8, all quotas are in principle on a global basis. A special quota system, however, is applied to imports of fishes and shellfishes caught in coastal waters of South Korea; they can be imported within a fixed total value.

In terms of total value, shrimp (from the People's Republic of China, United States, Mexico, Thailand, and a number of other sources) has been the number one import item in recent years. Other important products imported are fish meal from Peru and South Africa, dry laver from South Korea, cuttlefish and octopus from West African fisheries (presumably shipped through Las Palmas), and tunas from Taiwan, Ryukyu, and South Korea.

Reviewing the actual quotas applied, it is obvious that import restrictions are still quite severe for some products. The amount of laver imported from South Korea has been controlled strictly to protect domestic laver culture, which is one of the most important sectors of the Japanese fishing industry. The amount of imported fish meal is also controlled to protect fish meal manufacturing in Japan both aboard factoryships and ashore. In addition, the quantity of fish that can be purchased from foreign countries as raw material for fish meal (mainly pollack from the Soviet Union) is restricted. Some of the products which fetch extremely high prices are also tightly controlled. These include herring roe, as well as herring used for making dry herring and roe, cod and pollack roe, cuttlefish from West Africa, and some others.

Excepting laver, imports from South Korea are decreasing due largely to limited production in Korean coastal waters and growing domestic demand in Korea. In 1970, mackerels and jack mackerels, which had previously been excluded from items to be imported, were added to the list of products under the special value quota. The actual imports of these two forms in 1970 were very little because of strong demand in Korea. Future trend may be for the import of cultured oysters (just started) and clams, since Korea has a great potential for aquaculture in shallow waters. As Korea plans to expand her distant-water trawl fisheries in the North Pacific and West Africa, there may be pressure for increased imports of products from this source. Presumably, they will come under the global quotas of respective items.

Quotas for individual items are determined through consultations between the Ministry of Trade and the Fishery Agency of the Ministry of Agriculture and Forestry. The former normally presses for liberalization while the latter tends to resist it. In the case of fish meal imports, there is a conflict within the Ministry of Agriculture and Forestry, namely between the Fishery Agency and the Livestock Bureau, since the poultry and livestock industries in Japan want complete decontrol of fish meal imports.

Import duties on fishery products are in principle 10% on fresh and frozen items, 15% on salted and smoked items, and 20% on canned and related items. Duties on many AA items have been reduced gradually under the Kennedy Round system.

Further import decontrol is highly desirable and almost inevitable. Fish meal imports are due to be decontrolled, to a large extent, in the near future. The present plan is to determine, through consultations between the Fishery Agency and the Livestock Bureau, the amount of meal to be imported duty free, and to tax heavily any additional imports (in the neighborhood of $56 a ton). The effects of this measure will depend largely on the amount to be fixed for duty-free imports. If the quantity determined is high enough, the net effect will be almost complete decontrol. If, on the other hand, the amount is adjusted to protect domestic manufacturers, the situation will not be too different from what it is now.

A further step which should be considered is the relaxation of restrictions on pollack imports. The Soviet Union now produces a large quantity of pollack (mainly in waters off Kamchatka), 598,000 metric tons in 1969 as compared with 1,944,000 tons caught by Japan. (Including the North Korean catch, the total yield of Pacific pollack probably exceeded 3 million tons in 1970.) Presumably, most of the Russian pollack catch goes into fish meal. If the Soviet Union can export pollack to Japan for surimi manufacturing, the value of the Soviet catch would increase very substantially. The Japanese government allows the import of raw material for fish meal, practically all pollack, within a global quota of 45,000 metric tons. Although it is a global quota, the only country that can export pollack to Japan is the Soviet Union. A further strict condition is attached to pollack imports: fish must be processed into fish meal, fish oil, and solubles aboard Japanese ships before entering Japan. Initially, even production of pollack roe was prohibited, but this restriction was removed later. For the last 7 years, pollack have been purchased in west Kamchatka, the main Soviet fishing area, and processed on a Japanese factoryship. The price has been increasing gradually, and the Japanese company conducting this operation has been requesting the government to allow production of surimi, but this has not been approved. It is very difficult to understand why the processing of only 45,000 tons of pollack into surimi would do any harm to Japanese fishing companies or processors.

The basic question here is far beyond that of manufacturing a small amount of surimi under the present quota. Pollack fishing for surimi production is now the mainstay of the Japanese distant-water trawl fisheries. Demand for surimi is strong, and the pollack catch is going to level off sooner or later. Further intensification of Hokutensen fishing and Soviet fishing, and the expected expansion of the Korean fleet, will result in a sharp increase in fishing intensity in Kamchatka and North Kurile waters. Catch limits will become necessary, and I would not be surprised if the Soviet Union pressed for them in the near future. In the long run, it would be beneficial to Japan to increase, if necessary gradually, the purchase of pollack from the Soviet Union for surimi production. It would help meet growing demand; the value added in processing and marketing would be far greater than the value of raw material realized by the Soviet Union;[32] increased imports from the Soviet Union would perhaps alleviate international fishery problems between the two nations. It is not certain what South Korea will do with increasing pollack catches. As pollack, processed into dry fish, has always been highly valued in Korea (both North and South), it is likely that the

[32] The Soviet Union may already be producing surimi using imported Japanese equipment.

catches will be absorbed in Korean domestic markets. However, the Korean operators might try to export some of their catches to Japan or even develop their own surimi industry.

Further liberalization is in order for the import of products from South Korean coastal fisheries. Pressure from the Japanese laver culture industry is so strong that the Japanese government will not immediately relax restrictions on laver, but the present quota system for non-aquaculture products will become rather meaningless.

Another important item to be reconsidered is herring and herring roe. After the collapse of Japanese herring fisheries (Kasahara, 1961), domestic production of herring (mainly in Hokkaido) has become insignificant. Most of the Japanese catch now comes from waters off the coast of the Soviet Union and from the eastern Bering Sea. To meet part of the demand for herring roe and a dried herring product called "migaki," herring has been imported mainly from the Soviet Union either through transshipment on Soviet fishing grounds or as frozen herring. A small amount of frozen herring has also been imported from Alaska. A separate quota has applied to herring roe, the price of which is extremely high in Japan. Japanese companies initially had difficulties in teaching people in Alaska and Canada how to process herring roe, but the business is now firmly established along the coast from Alaska to the State of Washington. Importation of herring has been done through the Federation of Hokkaido Fishery Cooperatives acting as sole import agent. This system was adopted originally to minimize objections from Hokkaido fishermen. Importation of roe, on the other hand, is done by companies.

Herring fishing off the Soviet coast is now subject to severe restrictions under an agreement concluded in 1971. The amount taken by the mothership fishery in the eastern Bering Sea is still limited. The Hokkaido herring stock shows no sign of recovery. Import quotas are still low, 8,000 tons for herring and 500 tons for herring roe. The Japanese population is suffering from a ridiculously high price of roe. The present total consumption of herring products is only a small fraction of what it used to be before the collapse of the Japanese herring fisheries. Except for protecting the vested interest of Hokkaido fishermen, there is no social or economic justification for continuing the present system. Also questionable is an import quota for West African cuttlefish.

In addition to herring, most of the coastal pelagic species are also on the IQ list, including fresh, frozen, and most forms of processed products other than canned fish. Considering the rather small catches of these species made in the neighboring countries, I doubt that these restrictions have real significance. In short, it is about time for Japan to reconsider all trade restrictions on fishery products with a view to facilitating their import, even at the expense of the temporary suffering of some of the domestic fisheries, for increased imports would be beneficial to the population in general. There is a real danger of many of the fishery products becoming luxury items rather than main sources of animal protein supply for the population. This is already happening to a variety of products which were low- or medium-priced items only 10 to 15 years ago. The rapid development of a modern chicken industry in Japan, combined with the liberalization of meat and poultry imports, may make fishery products less and less important as main sources of animal protein.

Although the import quota system has been a major obstacle to the expansion of fishery imports, there are other problems also. The lack of know-how to produce products suitable for Japanese markets, for example, has made it difficult for many foreign countries to exploit export potentials. Except for such international commodities as fish meal, frozen shrimp, tuna, or canned fish, fishery products sold in Japan are very specific as to the method of processing and the quality of final products. The nature of the difficulty is demonstrated by problems which Japanese companies have encountered in the process of developing salmon and herring roe business in North America. In Peru, where anchovies are extremely abundant and cheap, nobody even thought of developing export business to exploit the Japanese market for boil-dried anchovies ("niboshi"). In the Far East and

Southeast Asia, domestic demand for fish is generally quite strong and most of the catches are consumed locally, except for such high-priced international commodities as shrimp or tuna. Some of these nations, particularly the Philippines and Ceylon, import large quantities of fishery products, some of them from Japan. There is no great surplus of low-priced fish in this general region.

The proportion of the combined value of fishery products in the total export value of Japan has been decreasing steadily, only 2.7% in 1968 and perhaps around 2% by 1971. Major export items in recent years have been frozen tuna, other frozen products, canned tuna, canned salmon, canned mackerel, and other canned products. Domestic demand for tuna is growing. Even canned albacore, which used to be a product entirely for export, is now consumed in a substantial quantity.

The Japanese people are extremely flexible in their consumption of fishes, and there is some demand for just about everything coming out of the sea. There are, however, certain trends of consumer preference that have become fairly obvious in the most recent years. First, demand for high-priced fishery products, such as raw tuna meat (particularly bluefin), shrimps, crabs, certain species of cephalopods, salmon, salmon and herring roe, certain species of flounders, yellowtail, eels, and a variety of species produced in inshore waters, is becoming stronger as the standard of living rises rapidly. Since most of these forms have limited supplies, their prices are pushed up sharply, more or less in proportion to the increase in the per capita income. Second, the sale of frozen seafood is going up very fast. This is, to a large extent, because of tremendous improvements made in recent years in the quality of frozen seafood through the introduction of better equipment. Third, demand for fish ham and sausage, which used to be very high, is now going down. This may be due to a greater consumption of true ham and sausage. Fourth, the production and consumption of traditional fish cakes, such as "kamaboko," "chikuwa," and their relatives using "surimi" as material, have gone up sharply as the supply of pollack surimi increased. Use of other species than pollack for these products has decreased at the same time. Fifth, demand for fish meal as feeds for livestock, poultry, and aquaculture is very strong. It is met largely from three sources: pollack, mackerel, and imports. It is obvious that further increases in fish meal consumption will have to be met largely from imports, although domestic production may also grow further.

Even in Japan, large fluctuations in the catches of pelagic species are real problems. For example, the total catch of saury in 1970 was only 85,000 metric tons, as compared with over half a million tons in 1959, but in value the catch was the second largest in history because of the high price of saury, which used to be one of the cheapest fishes. Much of the sharply increasing catch of mackerel has gone into fish meal and oil, with smaller quantities used for direct consumption and canning, the latter mostly for export.

Conclusions

Examining sector by sector, the future of the Japanese fishing industry in general, and distant-water fisheries in particular, does not seem bright. Possibilities for further expansion are limited.

In inshore waters, major efforts are required to minimize the effects of pollution on the productivity of fishing and aquaculture. For coastal and offshore fisheries around the Japanese islands, better management could improve the efficiency of fishing and perhaps total production. The desirability of further decreasing the fishing effort of coastal trawl fisheries is obvious. For coastal pelagic species which make up the greatest portion of the catch from waters around Japan, management strategies based on scientific research have not yet been established, and the fisheries are always subject to large fluctuations in the catches of a few important species.

Distant-water fisheries are facing more and more difficult international problems, and due to a general trend of extension of national jurisdiction, further restrictions are expected. More exploratory fishing (particularly deepwater trawling), joint ventures, fishing in waters of national jurisdiction under conditions set by

coastal states, and development of foreign fisheries through investment by Japan, provide partial answers, and these lines will undoubtedly be pursued. The period of rapid expansion of distant-water fisheries, however, is practically over. The pollack stocks in the North Pacific, on which almost the entire Japanese trawl fisheries in that region depend, are being fished with increasing intensity. With the expansion of Soviet fishing and the entry of a large Korean trawl fleet, problems of conservation and allocation are likely to become major international issues in the near future.

Japan has made little progress in the exploitation of abundant resources of unconventional species. Although such a possibility might be explored more vigorously in the future, it would not solve most of the problems faced by the fishing industry. Further decontrol of the import of fishery products and increased import quotas will provide effective means to meet immediate problems of supply shortage and high prices. In general, too, the future of the Japanese fishing industry should be considered in the context of the rapidly expanding economy of this highly industrialized country. Labor shortage will become further acute, making many types of fishing economically infeasible. Japan, however, has two advantages over many of the other nations: the government has effective means to control the industry and the nation has strong domestic demands for a great variety of fishery products. The Japanese fishing industry will continue to be a competitive one on the international scene for some time to come although it will have to undergo many changes to meet new problems.

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MIGRATION AND DISTRIBUTION OF WHITE MARLIN AND BLUE MARLIN IN THE ATLANTIC OCEAN[1]

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ABSTRACT

Migration and distribution of white marlin, *Tetrapturus albidus* Poey, and blue marlin, *Makaira nigricans* Lacépède, in the Atlantic Ocean are discussed on the basis of tagging data (western North Atlantic, 1954-May 1970) and statistics of the Japanese Atlantic longline fishery (1956-67). White and blue marlins are widely distributed over the warmer waters of the Atlantic. Seasonal concentrations occur in certain areas, especially in the western Atlantic.

In the North Atlantic one group of white marlin summers off the U.S. middle Atlantic coast. In the fall fish of this group migrate offshore, then south to winter off the north coast of South America. In the spring these fish return north along or through the Antilles and the Bahamas. Tagged fish from this group were recaptured after up to 4 years at liberty; the returns suggest that the annual mortality is between 14% and 39%. There are apparently other groups of white marlin in the North Atlantic that move seasonally between various localities, but these movements have not been fully defined. An apparently separate population of white marlin concentrates in the eastern South Atlantic Ocean in winter and in the western part in summer.

Blue marlin concentrate in the Caribbean Sea, the Gulf of Mexico and the North Atlantic south of lat 30°N, from June through October, and in the western and central South Atlantic between lat 10° and lat 20°S from February through April. These concentrations probably represent distinct spawning populations.

The white marlin, *Tetrapturus albidus* Poey, and the blue marlin, *Makaira nigricans* Lacépède (family Istiophoridae), are distributed widely in the Atlantic Ocean. Their distribution and habits are of interest because they are important game fishes and because they are taken by commercial longline fisheries.

Few studies have been made of the migration and distribution of either species in the Atlantic Ocean. Gibbs (1957) described in detail the distribution of white marlin in the Gulf of Mexico from catch records of the U.S. exploratory fishing vessel *Oregon*. Squire (1962) described the distribution of white and blue marlins in the western North Atlantic, based on longline catches of exploratory fishing vessels. De Sylva and Davis (1963) reported on their studies of the white marlin sport fishery off the middle Atlantic coast of the United States. Nakamura, Iwai, and Matsubara (1968) gave a general review of the billfishes of the world.

Ueyanagi et al. (1970) described the distribution, spawning, and relative abundance of billfishes in the Atlantic Ocean; this comprehensive work is based mainly on the results of the Japanese longline fishery and of cruises by Japanese research vessels.

Other reports are based mainly on incidental collections or the results of scattered fishing activity (LaMonte, 1955, 1958a, b; Erdman, 1956, 1962; Krumholz, 1958; Krumholz and de Sylva, 1958; de Sylva, 1958, 1963; Rodriguez-Roda and Howard, 1962; and Talbot and Penrith, 1962).

Sportsmen participating in the Cooperative Game Fish Tagging Program of the Woods Hole

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Oceanographic Institution began tagging marlins and other pelagic fishes in the western North Atlantic in 1954. Preliminary results of the program, pertaining to marlins, were described by Mather (1960, 1967, 1969). In 1956, Japanese longline vessels began fishing for tunas and billfishes in the Atlantic Ocean; this fishery soon expanded to cover all of the tropical and temperate Atlantic. Tag returns and records of catches from the longline fishery have provided detailed data on the distribution, movements, and relative abundance of white and blue marlins in the Atlantic. The results of our study of these data are presented here.

SPORT FISHERY

Sport fishing for marlins and other big game fishes developed along the Atlantic coast of North America and off the Bahamas and Cuba during the 1930's (Figure 1). After 1945, fishing spread to the Gulf of Mexico, the Caribbean, and more distant areas. The growth of the fishery was aided by the widespread prosperity of the era and by improvements in fishing boats and equipment. More white marlin than blue marlin are taken by sportsmen; however, the comparative scarcity and the challenging size and power of blue marlin make them the more highly prized trophy.

White and blue marlins share a vast habitat in the Atlantic Ocean. The white marlin ranges farther into the temperate zones during the warm seasons and congregates seasonally in certain coastal areas in much greater numbers than does the blue marlin. Along the east coast of the United States, white marlin are abundant during the warm season from Cape Hatteras, N.C., north to Cape Cod, Mass., but blue marlin are rarely caught north of Cape Hatteras.

Fishing for white marlin off the middle Atlantic coast of the United States originated in Maryland in 1935, and spread to Cape Hatteras and Cape Cod. The greatest fishing effort and the largest catches are still made off Maryland, Delaware, and adjacent parts of New Jersey and Virginia. The major fishing centers are Ocean City, Md., and the New Jersey ports from Cape May northward to Atlantic City. The most productive fishing grounds are Baltimore and Wilmington Canyons. Boats from nearly all ports on or near the Atlantic Ocean from northern Virginia to Cape Hatteras take white marlin, but Oregon Inlet, N.C., is the major fishing center south of Ocean City. White marlin are relatively scarce in coastal waters off northern New Jersey and western Long Island, N.Y., but often provide good fishing at Hudson Canyon, and from eastern Long Island to Nantucket, Mass., the northeastern limit of their coastal range. As noted above, the occurrence of white marlin from Cape Hatteras to Cape Cod is generally limited to summer.

The first sport fishery for blue marlin off the U.S. coast developed at Hatteras, N.C., in the late 1930's. Another major center for blue marlin fishing off North Carolina is at Morehead City, also mainly in late spring and summer.

White and blue marlins are occasionally taken off southeastern Florida and the Florida Keys, usually by anglers seeking sailfish, but the number caught is small compared to the fishing effort. The best fishing for white marlin in the Florida area is in spring.

Marlin fishing developed off the northwestern Bahamas in the 1930's. Both species of marlin are fished from a number of localities in the Bahamas throughout the year—white marlin being most abundant in spring, blue marlin in late spring and early summer. Sport fishing for marlins has been excellent off Havana, Cuba, in seasons similar to those in the Bahamas, but this activity has diminished in the past decade.

White and blue marlins are available throughout the Caribbean Sea, and sport fishing facilities have been developed in many localities. The oldest and most important center is the Venezuelan coast in the vicinity of La Guaira, where marlin fishing became popular soon after 1945. Fishing is excellent for white marlin in late summer and early fall, and for blue marlin in winter and spring. Fishing facilities for marlin also exist at many other localities, including the Virgin Islands, Puerto Rico, and Jamaica. Blue marlin usually are more abundant than white marlin off these islands. The best seasons usually are fall for small blue marlin, spring and early summer for large.

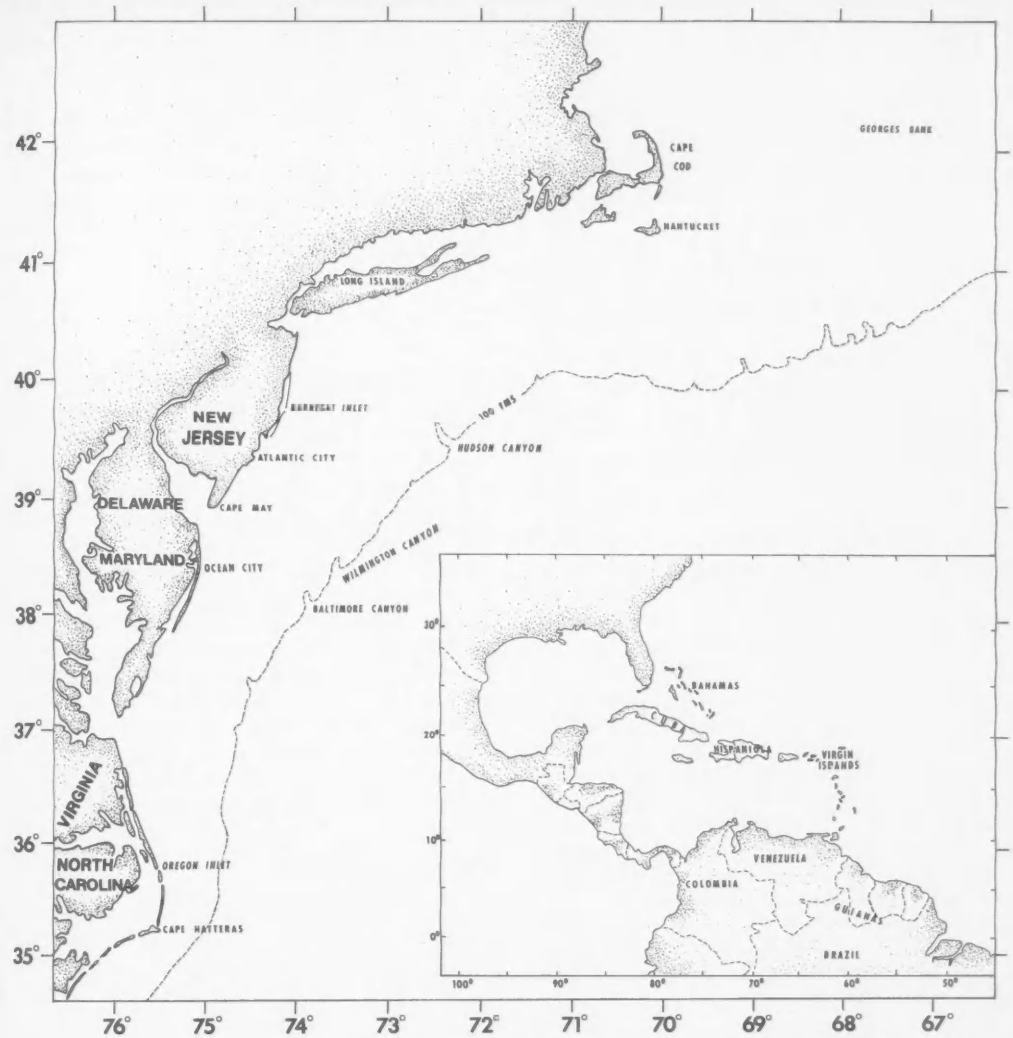

FIGURE 1.—The western North Atlantic Ocean, showing localities and areas of particular interest in the present study.

Marlin fishing in the Gulf of Mexico developed in the late 1950's off the Mississippi Delta, largely as a result of exploratory fishing catches of the Bureau of Commercial Fisheries vessel *Oregon*. The fishing season extends from early June into October, with a peak in July. In the late 1960's, a very productive area, centered on the De Soto Canyon in the northeastern Gulf, was fished from ports in western Florida and Alabama. This fishery also extends from June into October, but peaks in August. In 1969, some boats from Texas extended their operations farther offshore to the edge of the continental shelf and caught marlins consistently there for the first time.

Although most of the centers of sport fishing for marlin in the Atlantic are on the American coasts from Venezuela to Massachusetts, or on adjacent islands, there are several in other localities, such as Bermuda, the Azores, Rio de Janeiro in Brazil, and Cape Town in South Africa.

TAGGING STUDIES

METHODS

Cooperating fishermen marked white and blue marlins caught on rod and reel with dart tags as described by Mather (1963). Since this procedure does not require handling the fish or removing them from the water, their sizes were estimated. Tags and applicator poles were distributed to sportsmen by the Woods Hole Oceanographic Institution, either directly or through clubs and fishing tournament committees. Interest in tagging was stimulated by the press, radio, and television and also by clubs or tournament committees which offered incentives for tagging.

The tags carried the legend "reward" and the address of the Institution. (The fishermen often were more interested in receiving information on the tagged fish than in obtaining the $5 reward.) Posters were displayed where anglers gathered, and contact was maintained with fishery research agencies to which tags were apt to be returned. Some fishermen believed that the information gained from tagging hurt them and helped others. However, the volume of tagging and the percentage of returns increased over the years as more fishermen became aware of the program, and the mounting pressure by increased commercial fishing effort on the stocks demonstrated to fishermen the need for information on migratory patterns, population identity, and the effects of fishing.

WHITE MARLIN

A total of 6,590 white marlin were tagged and released in the western North Atlantic from 1954 through 1969; 65 tags have been returned as of June 1, 1970 (Table 1 and Appendix). Most releases (5,340) were made off the middle Atlantic coast of the United States from Cape Hatteras to Cape Cod. Other release sites were off southeastern Florida and the Bahamas, off Venezuela and in nearby waters, in the West Indies (Virgin Islands and Puerto Rico), in the northern Gulf of Mexico, and in the oceanic North Atlantic. Of the 65 tag recoveries, 41 were by commercial fishermen and 24 by sportsmen (Table 2). Before 1968, the Japanese longline fishery was the largest longline fishery in the Atlantic and covered nearly the entire ocean, but only 13 tags from white marlin have been returned from this

TABLE 1.—Releases (after slash) and returns (before slash) for white marlin tagged in the western North Atlantic Ocean by year and area of release.

Year	Area								Total	
	Hatteras to Chesapeake	Chesapeake to Barnegat	Barnegat to Cape Cod	Oceanic North Atlantic	SE Florida and W Bahamas	West Indies and vicinity	Gulf of Mexico	Venezuela and vicinity	Number	Percent
1954	--	--	0/4	--	--	--	--	--	0/4	0
1955	--	1/116	--	--	--	0/8	0/21	--	1/145	0.7
1956	--	1/402	--	--	--	0/3	0/8	--	1/413	0.2
1957	0/3	0/140	0/1	0/1	--	--	--	--	0/145	0
1958	0/1	0/39	0/1	--	--	--	--	--	0/41	0
1959	--	0/190	0/10	--	--	--	--	0/2	0/202	0
1960	--	0/96	0/2	--	0/4	0/1	0/4	0/4	0/111	0
1961	0/2	2/187	0/10	--	0/13	0/9	0/11	0/30	2/262	0.8
1962	0/30	4/294	0/18	--	0/41	--	0/4	--	4/387	1.0
1963	0/75	4/533	0/4	0/3	0/35	--	0/10	--	4/660	0.6
1964	4/182	8/258	0/1	0/5	1/67	--	0/13	--	13/526	2.5
1965	0/15	6/258	0/5	--	0/69	0/5	0/8	2/25	8/385	2.1
1966	1/36	7/172	1/64	0/6	1/54	0/4	0/23	1/149	11/508	2.2
1967	0/37	3/234	0/6	--	0/88	0/7	1/46	0/103	4/521	0.8
1968	1/100	8/569	0/32	--	0/94	0/16	0/56	0/16	9/883	1.0
1969	2/363	3/821	0/27	--	0/86	0/18	1/35	0/45	6/1,395	0.3
Unknown	1/1	1/1	--	--	--	--	--	--	2/2	
Total	9/845	48/4,310	1/185	0/15	2/551	0/71	2/239	3/374	65/6,590	

TABLE 2.—Returns from tagged white marlin, by fishery and nationality of recapturing vessel.

Type of fishery	Country	Number of returns
Sport fishery (rod and reel)	United States	24
Total		24
Commercial fishery (longline)	Canada	1
	Cuba[1]	14
	France	1
	Japan	13
	Norway	2
	South Korea	2
	United States	1
	Venezuela	7
Total		41
Grand total		65

[1] Some of the fish recaptured near Havana were caught by drift fishing from small boats with "criollo" lines. These usually consist of three interconnected lines with floats, each fishing at a different depth.

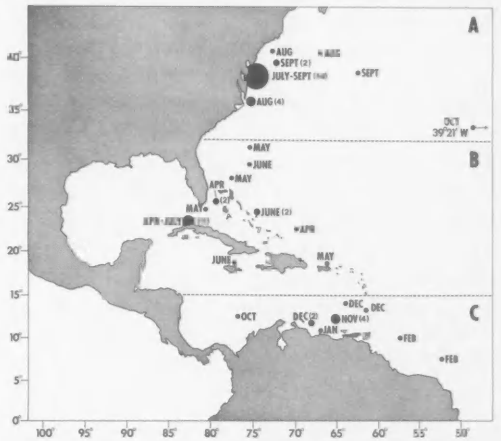

FIGURE 2.—Location of recaptures of white marlin tagged in the western North Atlantic Ocean north of lat 32°N between Cape Hatteras, N.C., and Cape Cod, Mass., in summer. The month of recapture is shown adjacent to each recapture site. The number of recaptures at each site is indicated by the number in parentheses (if more than 1) and by the size of the dot.

fishery. The Cuban and Venezuelan longline fisheries, though small compared to the Japanese fishery, accounted for 21 returns (14 and 7, respectively).

Tag recoveries from white marlin have been confined to the western North Atlantic. Of the 65 recoveries, 58 were from fish tagged off the middle Atlantic coast of the United States; we divided these into three groups on the basis of the area of recovery (Figure 2, Appendix):

Area A — North of lat 32°N
Area B — lat 15°N to lat 32° N
Area C — South of lat 15°N

In area A, 23 tagged marlin were recaptured in July through September and 1 in October; in area B, 22 were taken in April through July; and in area C, 12 were caught in October through February. The recaptures in the three areas are discussed below.

Area A

Of the 24 fish recaptured in area A, 14 were recaptured in coastal waters between Maryland and New Jersey. Twelve of these fish had been tagged locally (within 120 nautical miles of the point of recovery) and two had been tagged off Cape Hatteras. Of the fish tagged locally in July or August, three were recaptured in July or August of the same year; nine were recaptured in July or August of subsequent years. Time between tagging and recapture ranged from 9 days to 48 months. The 10 remaining fish tagged and recaptured in area A were recaptured in August, September, and October and at distances greater than 120 miles from the point of tagging. Some returns disclosed that in summer white marlin migrate along the east coast of the United States (Figure 3). Two fish tagged off Maryland and New Jersey were recaptured off North Carolina (150 and 200 miles distant) in 17 and 21 days, respectively. One white marlin traveled 500 miles, from off North Carolina to Georges Bank (off Cape Cod), in 12 days.

Two returns from considerable distances offshore showed that white marlin which range along the middle Atlantic coast in summer move offshore in the fall. One fish released off Maryland moved 580 miles eastward in 60 days, and the other, tagged in September 1966, was recaptured 25.3 months later at lat 33°15'N, long 39°21'W, about 1,800 miles east of Cape Hatteras.

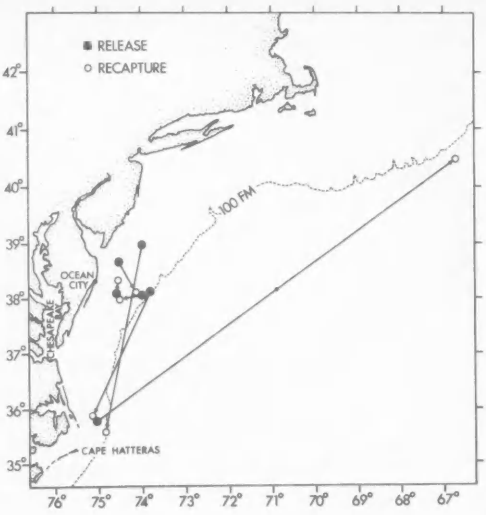

FIGURE 3.—Movements of tagged white marlin along the middle Atlantic coast of the United States, July-October. Recaptures were in the same year as releases.

Area B

Of the 22 white marlin recaptured in area B in April through July, 14 were taken in the Straits of Florida, 4 off the eastern Bahamas and eastern Greater Antilles, 3 were well off the southeast coast of the United States (between lat 28°N and lat 31°N), and 1 north of Jamaica.

Area C

Of the 12 tagged white marlin recaptured in area C, 1 was recovered in late October off Colombia, 9 were recovered in November, December, and January off Venezuela and the Lesser Antilles, and 2 in February off the Guianas.

The tagging results show clearly that white marlin in the western North Atlantic Ocean migrate seasonally. Fish tagged off the U.S. middle Atlantic coast apparently move offshore in late summer and fall from their summer grounds in coastal waters. They probably winter off the north coast of South America and move northward in spring back to the summer grounds. The large number of returns off Havana, Cuba, and the single return from north of Jamaica suggest that many move north through the Caribbean Sea and the Yucatan Channel. Four recoveries north of Puerto Rico and Hispaniola and east of the Bahamas indicate that white marlin also follow the Antilles Current[4] northward.

The nonrandom distribution of recoveries in areas A, B, and C reflects to some degree the seasonal nature of both the sport and commercial catches in those areas. In the Straits of Florida, however, tagged white marlin have been recaptured only in April through July even though the species is caught there throughout the year. Off the north coast of South America, white marlin are caught throughout the year by commercial and sport fishermen; yet tagged fish have been recaptured only in October through February.

The remaining 7 of the total of 65 returns were from 1,235 white marlin released from sport fishing centers in southeast Florida and the Bahamas (551 releases), the Gulf of Mexico (239), Venezuela (374), and the West Indies (71) (Table 1, Figure 4). Two white marlin tagged off Venezuela in August and September were recaptured after 3 to 4 months at large—one in November in the release area and the other in December off the coast of the Guianas. A third fish, tagged off Venezuela in October, was recaptured 20 months later (June) off South Carolina, probably en route to the U.S. middle Atlantic coastal region. Two white marlin tagged in the Bahamas were recaptured: one tagged in March was recaptured in June of the same year off St. Augustine, Fla., and the other, tagged in January, was recaptured in July in the Gulf of Mexico. Two white marlin tagged in July in the northern Gulf of Mexico were recaptured in the same area—one within a month and the other a year after tagging.

The two returns from off the eastern United States in June (from fish tagged in the Bahamas and off Venezuela) fit well with the indicated

[4] Names of currents are from Neumann and Pierson (1966).

FIGURE 4.—Location of releases and recaptures of white marlin tagged in the western North Atlantic Ocean south of lat 32°N. The months of release and recapture are shown in that order for each return. The number of recaptures at each site (if more than 1) is indicated in parentheses.

migratory pattern, but the remaining five do not. We do not now understand the relation between the nearly simultaneous summer and early fall concentrations of white marlin off the U.S. east coast and in the northern Gulf of Mexico. An interchange of fish between these two areas has not been demonstrated. None of the white marlin released in the Gulf of Mexico have been recaptured elsewhere, but a white marlin tagged in the Straits of Florida in January was recaptured in the Gulf of Mexico the following July. This recapture indicates that white marlin found off the northwestern Bahamas in winter may be a component of the summer concentration in the Gulf of Mexico. If this indication is correct, white marlin from the Bahamas could be migrating westward through the Straits of Florida while others en route to the U.S. middle Atlantic coast from the Caribbean are passing through the Straits to the east. White marlin are caught throughout the winter in the Bahamas, but fish tagged off Cape May-Cape Hatteras appear to migrate through the region only from early April to mid-July.

Tag returns indicate that white marlin off Venezuela in August and September remain off the north coast of South America into November and December, and that they are then joined by fish from the U.S. middle Atlantic coast. We are not sure how the marlin in the summer and early fall concentration off Venezuela are otherwise related to those in the summer and early fall concentrations in the Gulf of Mexico and off the U.S. middle Atlantic coast.

Early opinions that white marlin and other billfishes are short-lived and grow rapidly (Voss, 1956) are apparently true for Atlantic sailfish, *Istiophorus platypterus* (de Sylva, 1957), but de Sylva and Davis (1963) pointed out that white marlin may be long-lived. Their opinion was based on the weight-frequency distributions of fish in the U.S. sport fishery and the recovery of a tagged fish which had been at liberty for 4 years (Mather, 1960). The more recent information gained from tagging supports the belief of de Sylva and Davis (1963). Six tagged white marlin have been recaptured after 3 to 4 years at liberty. A comparison of sizes at release (estimated) and recapture does not indicate rapid growth after recruitment into the fishery.

We estimated the mortality rate of white marlin from tag-return data, using returns from white marlin tagged north of lat 32°N only (most fish were tagged in this area; those tagged in other areas might have had different migratory patterns). Moreover, we confined our consideration to returns from fish tagged in 1961 through 1965, because only two fish tagged before 1961 were recaptured and because returns from fish tagged after 1965 were incomplete. When the data were platted from white marlin recaptured from less than 1 month to more than 48 months after tagging, the recovery rates approximated an exponential relationship. The tag returns were grouped into time periods such as 0-12 months and 12-24 months, in view of a preliminary analysis which indicated that the returns within the first 6 months were in accord with the general pattern of returns

(Table 3, Figure 5). The indicated mortality rate was 27% per year, with 95 percent confidence limits of 14% and 39% (Z, the coefficient of instantaneous total mortality = 0.32 ± 0.17).

TABLE 3.—Summary of recaptures of tagged white marlin (to December 31, 1969). Dashed lines enclose data used for mortality estimates.

Year	Number tagged	Number recaptured[1]	Months at large				
			0-12	12-24	24-36	36-48	>48
1954	4						
1955	145	1					1
1956	413	1	1				
1957	145						
1958	41						
1959	202						
1960	111						
1961	262	2			1	1	
1962	387	4		2		2	
1963	660	4	2	1	1		
1964	526	12(13)	6(7)	2	3	1	
1965	385	6(8)	3(4)	2(3)	1		
1966	508	9(11)	4(6)	3	1	1	
1967	521	3(4)	1	(1)	2		
1968	883	9	6	3			
1969	1,395	5(6)	5(6)				
Unknown	2	2					
Total	6,590	58(65)	28(33)	13(15)	9	5	1
Total, 1961-65 only			11(13)	7(3)	6	4	

[1] Number recaptured are for groups A-C (see Appendix); numbers for groups A-D, if different, are shown in parentheses.

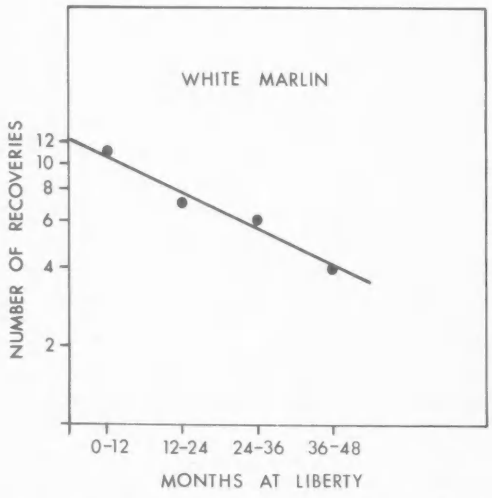

FIGURE 5.—Number of returns of white marlin tagged from 1961 to 1965 in waters north of lat 32°N, plotted by time at liberty.

BLUE MARLIN

Since 1954, 486 blue marlin have been tagged in the western North Atlantic; 3 have been recovered, all near their respective release points. One blue marlin released off Chub Cay, Bahamas, in August 1968, was recaptured off nearby Andros Island the following December; one released off La Guaira, Venezuela, in August 1966, was recaptured in the same area in October 1968; and one released off Biloxi, Miss., in June 1969, was recaptured 5 months later off Sabine Pass, La., 350 miles to the west. The returns indicate that meaningful information about blue marlin can be obtained if sufficient numbers are tagged.

LONGLINE CATCHES

METHODS

Data on the catch of marlins by the Japanese longline fishery in the Atlantic Ocean have been published by Shiohama, Myojin, and Sakamoto (1965) and by the Fisheries Agency of Japan (1966, 1967a, b, 1968, 1969). Catches of white and blue marlins, and those of other billfishes and tunas, are listed in those publications by 5°-quadrangles for each month, beginning in June 1956. Although catches in the categories "black marlin" and "striped marlin" also are listed, systematists do not presently recognize that black marlin, *Makaira indica*,[5] and striped marlin, *Tetrapturus audax*, occur in the Atlantic Ocean. We do not know whether those catches were misidentified or whether these species do, in fact, occur in the Atlantic. The catches listed in the two categories were too few to affect the conclusions of our study even if they were really white or blue marlin.

For each species, the catch per unit of effort (CUE), in fish per 100 hooks, was calculated for each 5°-quadrangle-month stratum in the period 1956-67 for which data were available. These CUE's were computed by dividing the number of fish caught in each such stratum by 1% of the number of hooks fished in it. To show seasonal distribution, average (unweighted)

[5] Ueyanagi et al. (1970) report occasional catches of *M. indica* in the equatorial and southeastern Atlantic.

CUE's for each 5°-quadrangle-month stratum were obtained by summing its yearly CUE's and dividing by the number of years.

The Japanese longline fishery in the Atlantic Ocean is directed primarily toward catching yellowfin tuna, *Thunnus albacares*, and albacore, *T. alalunga*, (Wise and Le Guen, 1969). Since marlins form only a small part (<3%) of the total catch of scombroid fishes, fishermen probably do not select specific fishing areas for marlins or adapt their fishing gear to catch marlins more effectively than other species. Possibly the catch rates for marlins are influenced by variations in the availability or the catchability of the fish, but the effects of such variations cannot be distinguished on the basis of the available data. We believe, therefore, that the catch rates by the longline fishery represent reasonably well the relative apparent abundance of marlins in the areas and seasons of intensive fishing. On this basis, we discuss distribution of white marlin and blue marlin in the Atlantic Ocean in the next sections.

WHITE MARLIN

The catches of the wide-ranging Japanese longline fishery show that white marlin are distributed over a much broader area than that indicated by returns from fish tagged in the sport fishery in the western North Atlantic Ocean. White marlin have been caught in all consistently fished areas of the Atlantic Ocean from lat 40°N to lat 40°S (Figure 6). The available data indicate that white marlin are scarce in both the north and south temperate zones in their respective winters (December-February and June-August).

Catch rates above 0.5 fish per 100 hooks are reported more often in the western than in the eastern Atlantic Ocean. We therefore conclude that although the distribution of white marlin is oceanwide, the species is more abundant in the western Atlantic. Sport fishermen report that white marlin are often concentrated at the edge of the continental shelf. Data from the longline fishery support this conclusion, inasmuch as the catch rates are generally higher in 5°-quadrangles adjacent to, or including, the edge of the shelf than in quadrangles in mid-ocean. No evidence has been found to date to suggest that the relative apparent abundance of white marlin in the Atlantic Ocean has been markedly affected by the longline fishery (Wise and Le Guen, 1969).

North Atlantic

In winter (December-February) white marlin are concentrated in the eastern Caribbean Sea and off the north coast of South America as far south as the equator. In spring some of these fish move northward into the Antilles Current beginning in March, and others move westward into the western Caribbean beginning in May and June. The northward movement of the first group conforms to the migrational pattern deduced previously from tag returns, but the second group appears to move into the northern and western Gulf of Mexico in summer, a pattern not supported by tagging data.

High catch rates in October, 300 to 1,200 miles off the east coast of the United States, support the hypothesis derived from tag returns —that white marlin summering off the U.S. mid-Atlantic coast move offshore in fall. In the Gulf of Mexico, however, white marlin are relatively abundant through October.

South Atlantic

In summer (December-February) white marlin are concentrated in the central South Atlantic Ocean and off the coast of Brazil. In the latter area, catch rates are among the highest known, occasionally reaching 3.8 white marlin per 100 hooks. In autumn (March-May) catch rates are generally lower than in summer and the marlin are not caught as far south. Because large areas of the South Atlantic are not fished in the autumn, catch rate data may not reflect a true picture of distribution. From June through September white marlin in the South Atlantic are concentrated in the South Equatorial Current and off the southwest coast of Africa. This season is the only one in which white marlin apparently are concentrated along the coast of Africa. From September through November,

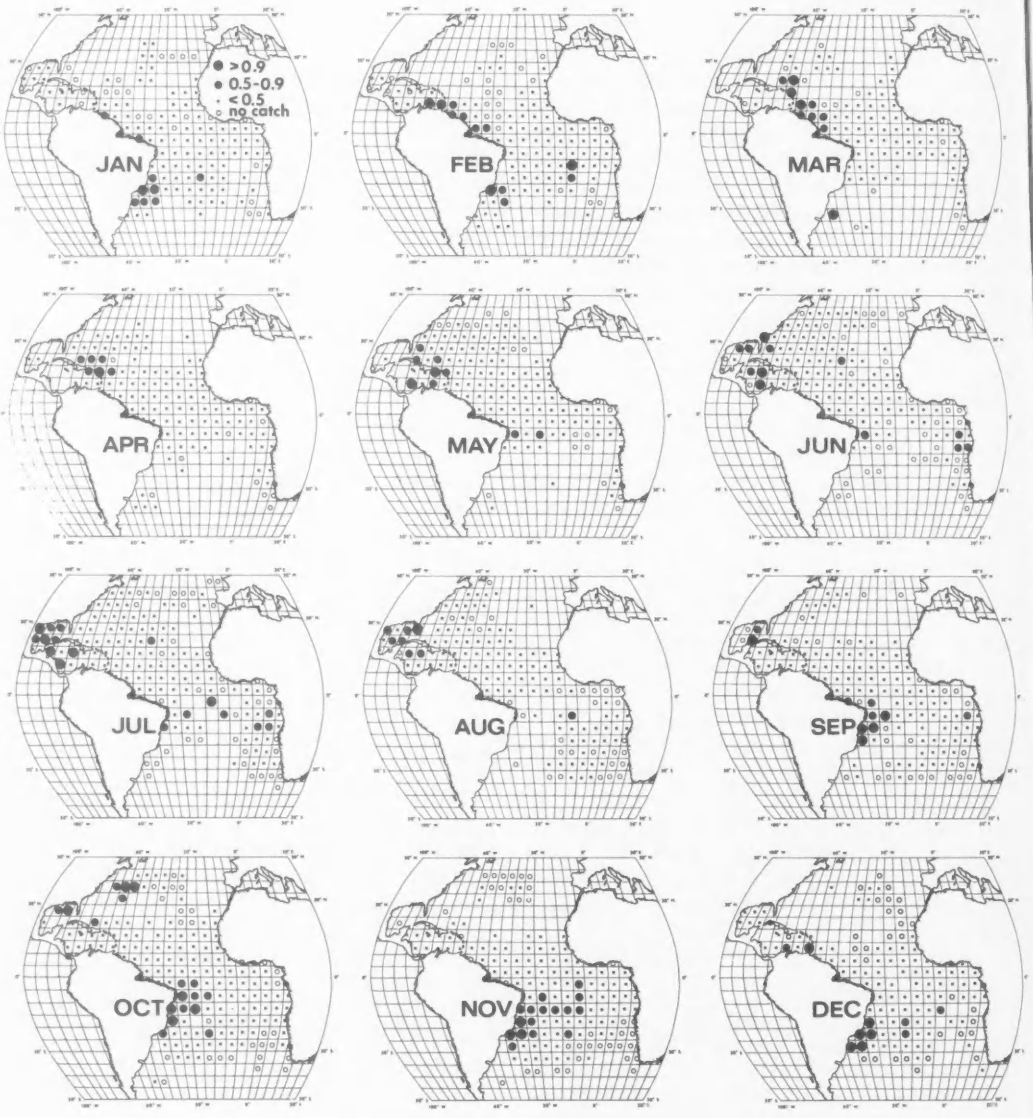

FIGURE 6.—Distribution and apparent relative abundance of white marlin in the Atlantic Ocean. Data are from records of the Japanese longline fishery, 1956-67. The catch per unit of effort (CUE) for each month in the rectangle is the arithmetic mean of the CUE of each month that the area in the rectangle was fished in the 12-year period. CUE is the number of fish caught per 100 hooks.

FIGURE 7.—Distribution and apparent relative abundance of blue marlin in the Atlantic Ocean. Data are from records of the Japanese longline fishery, 1956-1967. The catch per unit of effort (CUE) for each month in the rectangle is the arithmetic mean of the CUE of each month that the area in the rectangle was fished in the 12-year period. CUE is the number of fish caught per 100 hooks.

white marlin again are concentrated in the western South Atlantic off Brazil and in the South Equatorial Current.

We hypothesize that there are no major migrations of white marlin between the North and South Atlantic Oceans because the areas of concentrations of white marlin in the two oceans are generally separated by areas of low catch rates for white marlin and because not a single fish tagged in the North Atlantic has been recaptured in the South Atlantic. The North and South Atlantic groups of white marlin may be separate populations; Kamimura and Honma (1958a, b) believe that the closely related striped marlin of the Pacific Ocean has separate populations in the northern and southern hemispheres.

BLUE MARLIN

Monthly distribution of catches of blue marlin by Japanese longliners reveals two major seasonal concentrations in the Atlantic Ocean (Figure 7). In the Caribbean Sea, Gulf of Mexico, and the western North Atlantic Ocean south of lat 35°N, blue marlin are most abundant in the longline fishery from June through October. In the western and central South Atlantic Ocean, between lat 10° and lat 20°S, blue marlin are most abundant in February, March, and April. Possible migratory routes between the two areas are fished by the Japanese during all months of the year, but longline catches have produced no evidence that blue marlin move between the two oceanic regions. There may be two populations of blue marlin in the western Atlantic which are relatively unavailable to the longline fishery at certain seasons of the year, or there may be a single population which is unavailable to the fishery while the fish are migrating between the two areas. We believe that the two widely separated concentrations of blue marlin represent separate spawning populations. The evidence suggests that blue marlin in the North Atlantic spawn mainly from July through September and those in the South Atlantic spawn in February and March. It is unlikely that a single population of blue marlin would spawn at two widely separate locations at different times of the year. Eschmeyer and Bullis (1968) examined four larvae of blue marlin from the western North Atlantic captured in July and September, and Gehringer (1957) reported three larvae from the western North Atlantic and Gulf of Mexico in spring and summer, which were later identified as blue marlin by Ueyanagi and Yabe (1959). Caldwell (1962) reported on two postlarvae of blue marlin captured off Jamaica in September. Erdman (1968) concluded from his studies of gonad development and sex ratio that the peak spawning season for blue marlin off Puerto Rico was in July and August. In the South Atlantic, Bartlett and Haedrich (1968) reported on 85 larvae of blue marlin captured off the coast of Brazil in February and March. The size range was from 4.9 to 32.0 mm.

The blue marlin is apparently the only[8] billfish in the Atlantic whose abundance has been significantly affected by longline fishing. Wise and Le Guen (1969) showed significant rates of decline in relative apparent abundance of blue marlin in the two areas of major concentrations shown in Figure 7. They stated that these declines were associated with the intensive fishing for albacore and yellowfin tuna in the same areas. Ueyanagi et al. (1970) also reported a drastic decline in the apparent abundance of blue marlin in the Atlantic with the level of apparent abundance in 1965 only about one-fourth of that of 1962.

SUMMARY

WHITE MARLIN

1. Tag returns indicate that one group of white marlin moves from the middle Atlantic coast of the United States in summer to the north coast of South America in winter. The route appears to be initially offshore from the summer grounds, then south to the wintering area. The return is north in the vicinity of the Antilles and the Bahamas, including the Yucatan Channel and the Straits of Florida.

2. Longline catches support the above hypothesis but also indicate that a second group of

[8] Recent unpublished data suggest that the abundance of broadbill swordfish and white marlin in the Atlantic may also have been reduced by longline fishing.

white marlin moves from the wintering area off the coast of South America to summer grounds in the Gulf of Mexico. The relation between these two groups, which have different summering areas but similar wintering areas, is not clear, nor is their relation to a third group of white marlin which summers off Venezuela.

3. White marlin in the South Atlantic are separate from those in the North Atlantic and migrate from the eastern South Atlantic in winter to the western South Atlantic in summer.

4. White marlin appear to be relatively long-lived. An annual mortality of 27% was estimated from tag return data.

BLUE MARLIN

1. Only three tag returns have been recorded for blue marlin; all were relatively near the points of release.

2. Analysis of Japanese longline catch records for blue marlin reveals concentrations during summer and early autumn on the western side of the North and South Atlantic Oceans. In winter these concentrations disperse, and no pattern of distribution is apparent.

3. The two populations appear to be separate. We believe that spawning takes place in spring and summer for each group.

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The tagging results were made possible by the thousands of anglers, captains, and mates who have tagged and released many of their catches, and the clubs and tournament committees which have encouraged tagging. We regret that space does not permit individual acknowledgments here; the major participants are listed in the informal progress reports on the Cooperative Game Fish Tagging Program which are issued periodically by the WHOI. The press and the broadcasting media have also done much to encourage tagging and the return of tags.

[7] National Sea Grant Program, National Oceanic and Atmospheric Administration, Department of Commerce.

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APPENDIX

Release and recapture data for white marlin tagged in the western North Atlantic Ocean, 1954-69, are given in four Appendix Tables. Tagged fish are grouped by areas of release and recapture in order of recapture date. Data in parentheses were estimated by anglers at time of tagging. Although anglers estimated lengths in inches and weights in pounds, we have converted them to metric units.

APPENDIX TABLE 1.—Group A: White marlin tagged and recaptured north of lat 32°N.

Release data					Recapture data							
Date	Locality		Estimated size		Date	Locality		Size		Gear[1]	Flag	Months at liberty
	Lat N	Long W	Length	Weight		Lat N	Long W	Length	Weight			
			cm	*kg*				*cm*	*kg*			
July 11, 1955	(38°10′	74°45′)	(220)		July 18, 1959	37°31′	74°44′		(25.0)	RR	U.S.	48.2
July 31, 1962	(38°10′	74°45′)	(200)		Aug. 18, 1963	38°07′	74°52′	234	29.0	RR	U.S.	12.6
Aug. 7, 1961	37°53′	74°42′		(20)	Aug. 7, 1964	35°47′	75°05′	201	21.8	RR	U.S.	36.0
July 17, 1963	37°48′	74°41′		(12)	Aug. 9, 1964	(38°10′	74°45′)			RR	U.S.	12.8
July 30, 1964	35°47′	75°05′	(230)		Aug. 11, 1964	40°31′	66°45′		(16.8)	LL	Can.	0.4
July 27, 1964	(38°10′	74°45′)		(27)	Aug. 26, 1964	38°20′	74°38′			RR	U.S.	1.0
July 12, 1964	(38°10′	74°45′)		(18)	Sept. 10, 1964	38°40′	62°10′		(18.2)	LL	Jap.	2.0
July 28, 1962	37°50′	74°57′	(200)		Aug. 15, 1965	38°04′	74°47′	218		RR	U.S.	36.6
Aug. 7, 1965	38°42′	74°32′		(36)	Aug. 16, 1965	38°10′	74°10′	195	24	LL	Nor.	0.3
Aug. 2, 1964	36°05′	75°12′	(200)		Aug. 25, 1965	38°38′	74°25′	221	30.4	RR	U.S.	12.8
Aug. 26, 1963	(38°10′	74°45′)		(27)	Sept. 16, 1965	39°40′	72°20′			LL	Nor.	24.7
July 23, 1965	(38°51′	74°30′)	(200)		Aug. 4, 1966	40°45′	72°21′	226	30.4	RR	U.S.	12.4
July 17, 1966	38°58′	74°00′		(20)	Aug. 7, 1966	35°28′	74°52′	208	18.2	RR	U.S.	0.7
Aug. 24, 1964	(38°10′	74°45′)		(14)	Aug. 14, 1966	39°07′	74°25′	193	16.8	RR	U.S.	23.7
Aug. 18, 1964	36°00′	74°56′	(210)		Sept. 10, 1966	37°58′	74°55′	213	22.7	RR	U.S.	24.6
July 12, 1965	37°50′	74°57′	(210)	(18)	Sept. 13, 1966	39°31′	71°40′		31.8	LL	U.S.	14.1
July 9, 1968	(38°11′	74°00′)		(45)	Aug. 17, 1968	38°02′	74°35′	208	20.4	RR	U.S.	1.3
Sept. 13, 1966	38°30′	73°30′		(24)	Oct. 22, 1968	33°15′	39°21′	180		LL	S.K.	25.3
July 22, 1968	38°15′	73°50′	(220)		July 18, 1969	37°56′	74°40′	221	29.4	RR	U.S.	11.8
July 22, 1968	38°15′	73°50′		(20)	Aug. 4, 1969	38°15′	73°50′			RR	U.S.	12.4
Aug. 11, 1968	38°42′	74°25′		(18)	Aug. 6, 1969	36°12′	75°00′	(211)	(20.4)	RR	U.S.	11.8
July 21, 1968	37°26′	75°06′	(210)	(27)	Aug. 7, 1969	38°04′	74°10′	211	25.0	RR	U.S.	12.6
Aug. 13, 1969	38°13′	73°51′		(18)	Aug. 30, 1969	35°52′	75°12′	(203)	(25.0)	RR	U.S.	0.6
July 14, 1967	38°10′	74°32′		(23)	Aug. 31, 1969	37°31′	74°22′		(21.3)	RR	U.S.	25.6

[1] RR, rod and reel; LL, longline; CL, criollo line.

APPENDIX TABLE 2.—Group B: White marlin tagged north of lat 32°N and recaptured between lat 15°N and lat 32°N.

Release data					Recapture data							
Date	Locality		Estimated size		Date	Locality		Size		Gear[1]	Flag	Months at liberty
	Lat N	Long W	Length	Weight		Lat N	Long W	Length	Weight			
			cm	*kg*				*cm*	*kg*			
(Summer 1956)	(38°10′	74°45′)			Apr. 30, 1957	23°12′	82°05′		27.2	CL	Cuba	
Aug. 26, 1962	37°40′	74°54′	(210)		Apr. 8, 1964	23°11′	82°23′	218	25.0		Cuba	19.4
Sept. 6, 1961	38°14′	73°53′			May 5, 1964	23°14′	82°20′				Cuba	32.0
Aug. 29, 1963	38°02′	74°04′			May 8, 1964	23°13′	82°22′		22.7	CL	Cuba	8.3
Aug. 19, 1964	(38°10′	74°45′)			June 14, 1965	29°32′	75°13′			LL	Jap.	9.8
Aug. 1, 1964	38°30′	73°30′	(180)		June 27, 1965	24°23′	74°04′	(120)		LL	Jap.	10.9
Aug. 17, 1964	37°51′	74°58′		(18)	July 2, 1965	23°17′	82°21′		22.7		Cuba	10.5
July 1965	38°22′	74°30′		(36)	Apr. 2, 1966	25°42′	79°21′	234	40.9	RR	U.S.	(8.6)
(Aug. 1962)	(38°10′	74°45′)			Apr. , 1966	25°42′	79°21′		25.0	RR	U.S.	(43)
July 23, 1965	37°56′	74°40′		(32)	June 14, 1966	(23°15′	82°17′)		18.2		Cuba	10.7
July 21, 1966	(38°10′	74°45′)		(32)	May 5, 1967	31°10′	75°10′	220	30	LL	Cuba	9.5
July 4, 1966	38°30′	73°30′	(160)	(18)	May 28, 1967	23°05′	83°13′	200	25.0	CL	Cuba	10.8
Aug. 12, 1966	(39°18′	74°00′)		(20)	May 10, 1968	(23°05′	82°45′)	213	25.0	CL	Cuba	20.8
Aug. 9, 1966	40°52′	71°44′		(40)	May 18, 1968	18°38′	66°07′	234	40.9	RR	U.S.	21.2
July 17, 1965	38°09′	74°30′		(25)	June 20, 1968	23°14′	82°22′		35.8	CL	Cuba	35.1
Sept. 3, 1966	35°49′	74°56′	(200)		July 11, 1968	23°14′	81°55′	228	15.9	LL	Cuba	22.2
Aug. 18, 1964	38°47′	74°17′	(200)		July 20, 1968	23°10′	82°30′		15.0	CL	Cuba	47.0
Sept. 24, 1968	38°22′	73°41′		(27)	Apr. 27, 1969	22°40′	69°50′		23	LL	S.K.	7.0
Sept. 17, 1967	38°15′	73°50′			(May 15, 1969)	28°06′	77°16′		15	LL	Cuba	(20.5)
July 25, 1967	38°44′	74°29′	(230)	(27)	May 31, 1969	24°49′	80°29′	206	19.1	RR	U.S.	22.2
July 13, 1968	38°00′	74°00′		(18)	June 7, 1969	24°30′	74°40′	180	22.5	LL	Jap.	10.8
Aug. 23, 1968	35°47′	74°40′	(190)	(19)	June 21, 1969	18°45′	77°04′	170	20.0	LL	Jap.	9.9

[1] RR, rod and reel; LL, longline; CL, criollo line.

APPENDIX TABLE 3.—Group C: White marlin tagged north of lat 32°N and recaptured south of lat 15°N.

Release data					Recapture data							Months at liberty
Date	Locality		Estimated size		Date	Locality		Size		Gear[1]	Flag	
	Lat N	Long W	Length	Weight		Lat N	Long W	Length	Weight			
			cm	kg				cm	kg			
Aug. 8, 1963	38°50′	74°30′			Dec. 10, 1963	13°15′	61°30′		18.2	LL	Fr.	4.1
Aug. 20, 1964	35°50′	75°00′	(200)	(20)	Dec. 12, 1966	12°05′	67°55′		25.0	LL	Ven.	27.8
July 27, 1966	37°58′	74°38′		(18)	Jan. 2, 1967	10°55′	67°00′			LL	Ven.	5.2
Aug. 31, 1964	37°47′	74′49°		(17)	Feb. 15, 1967	07°25′	52°20′			LL	Ven.	29.5
Unknown	(36°00′	75°00′)			Nov. 8, 1968	12°30′	65°25′					
(Aug. 1, 1968)	38°15′	73°50′			Feb. 13, 1969	10°02′	57°22′	157	20.5	LL	Ven.	(6.6)
Aug. 4, 1969	36°12′	75°12′		(28)	Oct. 29, 1969	12°40′	76°53′		25			2.8
Aug. 12, 1969	(38°15′	73°50′)		(23)	Nov. 13, 1969	12°07′	64°50′		(17)	LL	Jap.	3.1
Unknown	(38°15′	73°50′)			Nov. 25, 1969	11°58′	65°14′		(20)	LL	Jap.	
July 24, 1966	37°59′	74°44′		(27)	Nov. 28, 1969	11°58′	65°14′		(20)	LL	Jap.	39.2
Aug. 18, 1969	(35°57′	75°01′)	(200)	(18)	Dec. 14, 1969	14°00′	64°00′	140	(15)	LL	Jap.	3.9
July 18, 1969	37°54′	74°36′		(20)	Dec. 16, 1969	11°25′	68°12′		(17)	LL	Jap.	5.0

[1] RR, rod and reel; LL, longline; CL, criollo line.

APPENDIX TABLE 4.—Group D: White marlin tagged south of lat 32°N.

Release data					Recapture data							Months at liberty
Date	Locality		Estimated size		Date	Locality		Size		Gear[1]	Flag	
	Lat N	Long W	Length	Weight		Lat N	Long W	Length	Weight			
			cm	kg				cm	kg			
Jan. 18, 1964	25°43′	79°20′		(23)	July 25, 1964	23°37′	92°37′		2.2	LL	Jap.	6.2
Aug. 21, 1965	(10°50′	66°55′)		(30)	Dec. 28, 1965	09°15′	57°50′	250	14.2	LL	Jap.	4.2
Mar. 24, 1966	(25°20′	77°58′)		(18)	June 3, 1966	29°35′	76°50′	210	20	LL	Jap.	2.3
Sept. 4, 1966	10°47′	66°57′		(20)	Nov. 25, 1966	10°55′	67°00′	160	22	LL	Ven.	2.7
Oct. 16, 1965	(10°50′	66°55′)		(25)	June 14, 1967	32°27′	76°00′	193	16	LL	Cuba	19.9
July 3, 1967	29°55′	86°46′	(210)	(27)	July 31, 1968	29°49′	87°17′	234		RR	U.S.	12.9
July 31, 1969	29°55′	87°05′	(200)	(20)	Aug. 13, 1969	29°51′	86°48′	201	25.0	RR	U.S.	0.4

[1] RR, rod and reel; LL, longline; CL, criollo line.

RETENTION OF LARVAL HERRING WITHIN THE SHEEPSCOT ESTUARY OF MAINE

JOSEPH J. GRAHAM[1]

ABSTRACT

This paper demonstrates a system of larval movements that retains larval herring within an estuary despite its seaward residual flow. Data are reviewed from a 2^3 factorial design using buoyed and anchored nets in a narrow channel of the estuary. Three factors were involved: location, tidal phase, and depth. Catch rates of larvae relative to these factors suggested that the larvae maintained their position in the upper portion of the estuary by (1) occupying the landward net tidal flow near the bottom, (2) moving upward upon reaching the limit of their landward penetration (3) then seaward in the net flow near the surface, and (4) finally descending again into the landward net flow.

Larval herring, *Clupea harengus harengus* Linnaeus, move up the Sheepscot estuary of Maine primarily in the autumn and spring. During these seasons the larvae accumulate in the upper portion of the lower estuary where they are retained despite the residual seaward flow of the estuary. Statistically significant differences in the distribution of larval herring according to depth and location and the interaction of these two factors with tide suggested that the larvae were using tidal flows to migrate (Graham and Davis, 1971). This paper examines the data, upon which the statistical results were based, to demonstrate a system of larval movements that retain the larvae within the estuary.

MATERIALS AND METHODS

Buoyed and anchored nets were fished (Figure 1); their construction and validity in sampling larval herring is noted briefly in this paper and is available in detail in another paper (Graham and Venno 1968). Four nets were attached to one line which was buoyed at the surface and anchored to the bottom to sample at predetermined depths (0, 10, 15, and 20 m). A flow meter measured the amount of water strained, from its central position in the mouth of each net. The mouth opening of the net was 0.5 m in diameter and the length of the net was 1.9 m. Mesh diameter was 0.75 mm. Filtration efficiencies of the net ranged from 80 to 90% at current speeds above 15 cm/sec and 100% within speeds from 15 to 3 cm/sec. Below 3 cm/sec the impeller of the flow meter does not revolve. Tests simulating sampling conditions showed that clogging did not change these filtration efficiencies.

The nets fished approximately 6 hr on the flood and 6 hr on the semidiurnal ebb tides. They were set at slack water during dusk, retrieved and reset at the end of the tidal stage during slack water. Two lines of nets were set at the landward end of the estuarine channel and two were set at the seaward end (Figure 2). The sampling area within the estuarine channel was 9 km long, 275 m wide, and about 20 m deep throughout its length. The distance between sets at the seaward end of the channel was 2 km, that between the landward sets was 3.2 km, and the distance between the two locations was 3.8 km as measured from the interior sets.

For a given line of nets catch rates were determined for the two nets above mid-depth and for the two nets below mid-depth. In each case, the total amount of water strained for the two nets above and below mid-depth was

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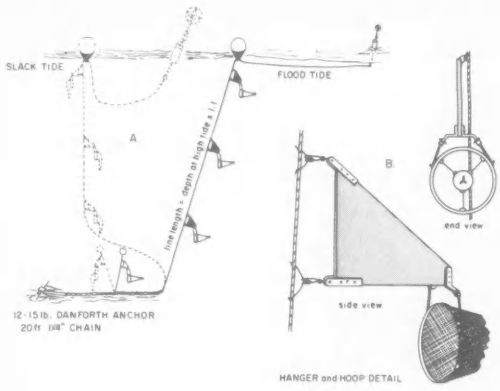

FIGURE 1.—Buoyed nets for sampling larval herring. A, positions of four nets during slack and flowing tides; B, arrangement of hanger and hoop (After Graham and Venno, 1968).

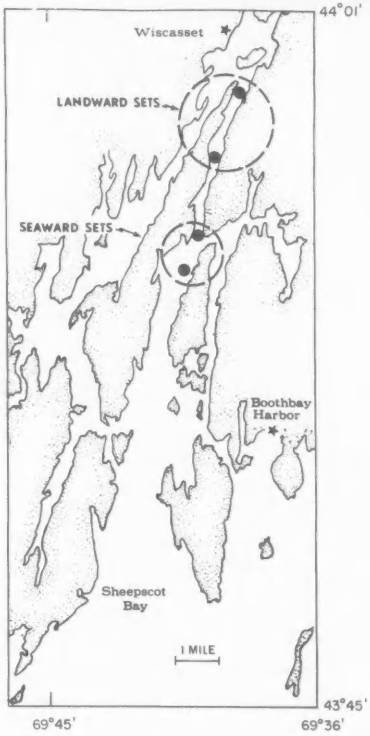

FIGURE 2.—Locations (circled) of buoyed and anchored nets in the Sheepscot estuary of Maine (after Graham and Davis, 1971).

divided into the total number of larvae captured and multiplied by 100 to obtain catches per 100 m^3. Thus, at each location (landward and seaward) average catch rates from the two lines of nets were obtained for two depths (shallow and deep) during two tidal stages (flood and ebb), providing eight samples for each location or 16 samples for a single overnight experiment.

The nets were fished during darkness because the larvae avoided the nets during daylight. A comparison of nighttime catches between two lines of buoyed nets set in tandem within the channel and a comparison between nighttime catches of buoyed nets with those of a high speed Boothbay Depressor Trawl (Graham, Chenoweth, and Davis, 1972) suggested that the larvae did not avoid the net at night nor did they escape from the nets during slack water. The average catches above and below mid-depth determined the concentration of larvae in the water layers above and below the level of no-net-motion of the tidal flows. Larvae in the upper layer would experience a net seaward transport and those in the lower layer would experience a net landward transport. In addition to sampling larvae already in the channel, the two lines of nets in the landward location would sample larvae transported into the channel by the ebb tide and the two lines in the seaward location would sample larvae transported into the channel by the flood tide.

The arrangement of the nets and catches in the estuarine channel constituted a factorial sampling design. A factorial design is especially adaptable to examining the effects of a number of different factors which vary in a regular way during an experiment. The source of regularity in the experiments was the tidal currents transporting the larvae. An example of the statistical procedures is given in Table 1. Catch rates were transformed into common logarithms to obtain a normal distribution of the data for computations. In this paper the untransformed catch

TABLE 1.—Statistical procedures for a 2^3 factorial design using larval catches per 100 m^3 of water strained from an experiment during Nov. 8, 1967. I) Factors are coded, II) Catches are assigned to the factorial order, III) the sums of squares are determined, IV) they are applied to an analysis of variance, and V) a conclusion is determined from the analysis.

I. *Factors and their codes (A).*

Tidal phase	(A)	flood	(+)	ebb	(−)
Water depth	(B)	shallow	(+)	deep	(−)
Location	(C)	landward	(+)	seaward	(−)

II. *Factorial order (1) of larval catches per 100 m^3.*

		Seaward location		Landward location	
Flood	Shallow	5.44(4)	9.78(4)	2.64(8)	5.54(8)
	Deep	11.53(2)	3.51(2)	86.09(6)	48.60(6)
		Seaward location		Landward location	
Ebb	Shallow	2.89(3)	6.29(3)	33.28(7)	24.73(7)
	Deep	0.44(1)	4.73(1)	26.75(5)	4.58(5)

III. *Determination of the sums of squares for the 2^3 factorial design using logarithms of the catches; 1 has been added to each characteristic.*

Factorial order		A	B	AB	C	AC	BC	ABC
(1) 0.6435	1.6749	−	−	+	−	+	+	−
(2) 2.0618	1.5453	+	−	−	−	−	+	+
(3) 1.4609	1.7987	−	+	−	−	+	−	+
(4) 1.7356	1.9903	+	+	+	−	−	−	−
(5) 2.4273	1.6609	−	−	+	+	−	−	+
(6) 2.9350	2.6866	+	−	−	+	+	−	−
(7) 2.5221	2.3932	−	+	−	+	−	+	−
(8) 1.4216	1.7435	+	+	+	+	+	+	+
Total =		+1.5382	−0.5694	−4.1060	+4.8792	−1.9718	−2.6984	−2.4612
Sums of squares (Total) $\frac{2}{16}$ =		0.1479	0.0203	1.0537	1.4879	0.2430	0.4521	0.3786

IV. *Analysis of variance.*

Factor	Sum of squares	Degrees of freedom	Variance	*F*-ratio
A	0.1479	1	0.1479	1.04
B	0.0203	1	0.0203	0.14
AB	1.0537	1	1.0537	7.40*
C	1.4879	1	1.4879	10.45*
AC	0.2430	1	0.2430	1.71
BC	0.4521	1	0.4521	3.17
ABC	0.3786	1	0.3786	2.66
Within	1.1394	8	0.1424	
Total	4.9229	15		

*Statistically significant, $P_{.05} = 5.32$

V. *Conclusion.*

Significantly more larvae were captured below mid-depth (deep) on the flood tide and more above mid-depth (shallow) on the ebb tide. In addition, significantly more larvae occurred at the landward location than at the seaward location.

rates are used because they are more familiar than logarithms as measures of concentrations of larval fishes in their environment. The results of the statistical analysis are given by Graham and Davis (1971). Significant differences between catch rates with depth and location and the interaction of these two factors with tide occurred primarily in the autumn and spring. Of eight experiments conducted from late October to early December (1965-67) five had significant differences between larval catch rates. Of 10 experiments completed between mid-March and mid-May (1966-68) six had significant differences between catch rates. The distributions of larvae from experiments that had significant differences in larval catch rates will be described, and an explanation for the absence of significance in the other experiments will be discussed.

RESULTS AND DISCUSSION

Concentrations of larval herring were evident within the channel when the distributions of catch rates that differed statistically within the

experiments were examined. The analysis of variance from an experiment on November 8, 1967 (Table 1, IV) showed that the catch rates of larvae differed significantly with location and with the interaction of depth and tide. The untransformed catch rates showed that concentrations of larvae were shallow during the ebb tide and deep during the flood tide. Also, more larvae occurred at the landward end of the channel than at the seaward end. These data and those from other experiments having significantly different distributions in catch were summarized in Table 2. For example, the interaction on November 8 was illustrated by first summing all of the cubic meters of water strained by the shallow nets and then all of the larvae captured by them. These totals were used to obtain an average catch per 100 m^3 of water strained; the process was repeated for the deep nets. Beginning anew, the average catch rates were determined for the two locations. The numbers in parentheses in Table 2 locate the concentrations of larvae within the channel diagrammed in Figure 3. Those concentrations of larvae captured in the shallow nets had a net transport seaward during an experiment and those in the deep nets were transported landward. A transition in such transport occurred for those larvae concentrated throughout the water column at one location or the other. The arrows in Figure 3 infer a system of movements from the location and transport of the larvae that appears analogous to those of other larval fishes (Pearcy and Richards, 1962) and planktonic organisms (Bousfield, 1955) which are retained in estuaries by tidal currents. The suggested movements

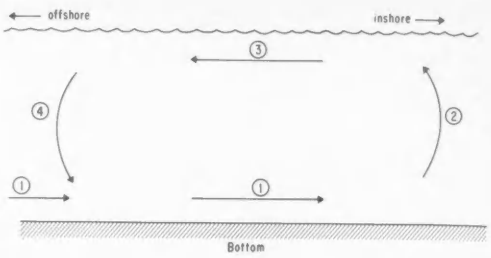

FIGURE 3.—Diagram of a system of larval movements thought to retain larval herring in the Sheepscot estuary. The numbered distributional components of the system coincide with the numbered catches in Table 2.

TABLE 2.—Catch rates from 11 experiments in the autumn and spring. The distributions of rates for single factors and for two factors (interaction X) are given. Numbers in parentheses are from Figure 3; unnumbered catch rates are discussed in the text.

Single factor—depth

	Dec. 7, 1967	*Mar. 20, 1967*	*May 4, 1967*
Shallow	1.95(3)	0.62	40.64(3)
Deep	0.60	7.15(1)	7.66

Single factor—location

	Nov. 8, 1967	*Nov. 21, 1966*	*Dec. 7, 1967*	*Mar. 14, 1968*
Landward	29.56(2)	20.76(2)	1.84(2)	6.16(2)
Seaward	6.60	11.43	1.26	2.06

Two factor—depth × tide

	Flood	*Ebb*	*Flood*	*Ebb*	*Flood*	*Ebb*
	Nov. 1, 1965		*Nov. 8, 1967*		*Nov. 21, 1966*	
Shallow	4.20	11.12(3)	6.11	18.57(3)	3.84	15.46(3)
	×		×		×	
Deep	10.40(1)	1.43	48.42(1)	18.17	34.85(1)	8.96
	Dec. 6, 1966		*Apr. 27, 1966*		*May 9, 1967*	
Shallow	10.08	4.03	16.74	14.53	18.80	4.40
	×		×		×	
Deep	1.48	7.94	8.74	20.84	2.78	12.10

Two factor—location × tide

	Flood	*Ebb*	*Flood*	*Ebb*
	Mar. 26, 1966		*Apr. 26, 1966*	
Landward	3.41	11.46(2)	16.98	15.28
	×		×	
Seaward	10.54(4)	1.66	9.32	27.27

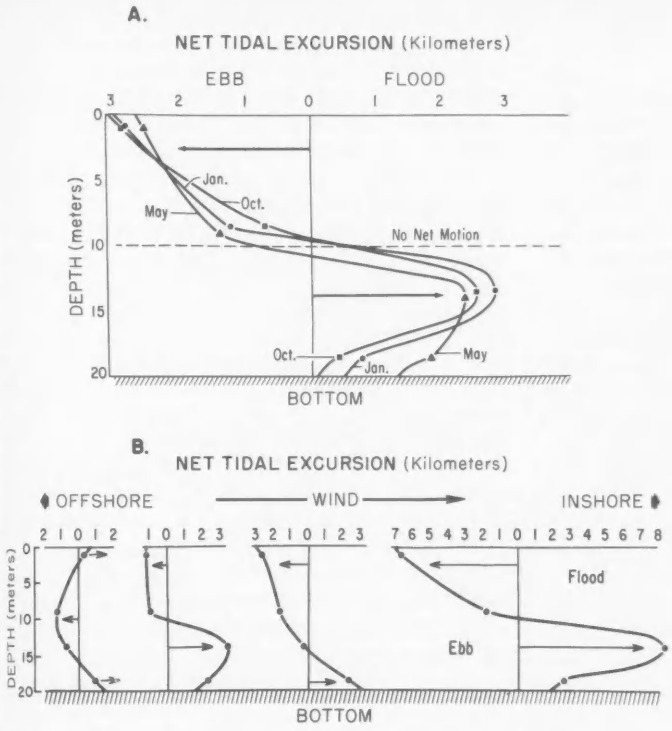

FIGURE 4.—A. Vertical profiles of mean tidal excursion for the four sets of buoyed nets in the estuary of the Sheepscot River (after Graham and Davis, 1971). B. An effect of onshore wind on the net tidal excursions for individual sets of nets in the estuary.

would retain the larvae within the channel after they had entered it on the net flood tide near the bottom.

The system of movements diagrammed in Figure 3 is based on the average two-layer semidiurnal tidal flow (Figure 4A). But the dynamics of estuarine flow can be changed by large amounts of freshwater discharge, wind direction and velocity, and the shape of the channel. Graham and Venno (1968) found that an increase in freshwater discharge and the shape of the channel could change considerably the catch of buoyed nets in the Sheepscot estuary. Although the nets were positioned in the experimental design to lessen such effects, three of the experiments had results that could not be attributed to the system of movements; they are unnumbered in Table 2. All three had interactions between depth and tide and in one case (April 27, 1966) between location and tide as well. The distribution of larval catches was opposite to that expected. For instance, catch rates were larger on the flood tide near the surface and on the ebb tide near the bottom. Because tide was involved in each case possibly these data resulted from unusual tidal dynamics. On May 9, 1967, tidal excursions were modified by winds. Winds blew landward and up the channel during the day preceding the setting of the nets and continued through the flood tide on the night the nets were set. Wind velocities were usually 10 to 20 knots with gusts up to 30 knots. Readings from flow meters showed a typically shaped profile of net tidal excursion at the most landward station (Figure 4B). This was progressively altered seaward until the last station

had a small net upstream flow at the surface. Apparently, the winds reversed the tidal flow to some extent and thus the larval distribution as well.

Although I cannot account with certainty for the system of larval movements in the sampling area, the most reasonable explanation is that the larvae responded to changes in the character of the tidal flow. Larvae are transported up the estuary at about 1.8 knots per semidiurnal tidal cycle (Graham and Davis, 1971) which approaches the average length of tidal excursions recorded at 15 m, below the level of no-net-motion. This level of no-net-motion is obliterated in the upper estuary where the maximum depth is 10 m and the channel widens and extensive mud flats are present. The transition zone between the lower and upper estuaries is near the town of Wiscasset (Figure 2) and coincides with the maximum shoreward penetration of an abundance of larvae. Stickney (1959) states that the upper estuary compared to the lower has a greater exchange ratio, lower and more variable salinity and a wider range in temperature. A reversing tidal falls 3.5 km above the transition zone completely mixes the water. The most likely agency to initiate the ascending response (Figure 3, No. 2) by the larvae would be the change in the character of the tidal flows caused by shoaling of the bottom rather than agencies peculiar to the estuary. Herring are retained throughout their larval life over the banks and ledges of the open waters of the Gulf of Maine where the water is shallow and the tidal flows are well developed but conditions are not estuarine. After a brief transport downstream near the surface the larvae would resume their usual transport by descending towards the bottom.

The results suggested that the arrangement of buoyed and anchored nets in the estuarine channel was appropriate to sampling larval herring transported within the tidal currents. Larvae were sampled efficiently on both the flood and ebb tides, since no important main effect was obtained for tidal phase during the experiments. To obtain such an effect would have required a larval concentration to pass beyond the positions of the nets; then the larvae would either have to miss the nets on the return tidal current or drift to some area in the channel where they were not subject to the currents. Because the larvae were transported by the tidal currents, tide was always one of the interacting factors and an interaction between depth and location was not obtained.

One explanation for the appropriateness of the sampling design was that concentrations of the larvae were of sufficient length to overlap a pair of nets when transported into a given location. When this occurred, the difference in catch rates between the two lines of nets within the location would be small, and the difference between the two lines of nets in the other location where the concentration did not occur would also be small. These differences within the locations provided a measure of experimental error in the sampling design and if small they would yield a statistically significant F-ratio when compared to differences in catch rates between location and depth and the interaction of these two factors with tidal phase (e.g., F = mean square between locations/mean square within locations). Statistical significance would not occur when a concentration overlapped only one line of nets in a given location; the differences in catch rates between the two lines of nets would be relatively large, as indicated for the exterior and interior nets of the seaward location in Table 3.

Although net tidal flows in the channel affected the transport of the larvae, temporal variations in tidal currents made it difficult to determine the exact nature of that transport. The catch rates and corresponding tidal excursions obtained from the nets were accumulative and

TABLE 3.—Larval catches per 100 m^3 of water strained from an experiment during March 28, 1968. When treated as in Table 1 the distributions of the catch rates were not statistically significant.

Tide	Depth	Seaward location		Landward location	
Flood	Shallow	2.35	7.74	4.46	4.32
	Deep	2.68	2.84	3.85	3.65
Ebb	Shallow	1.37	6.07	3.38	3.58
	Deep	1.40	11.09	3.79	5.87

did not represent the many changes that probably occurred in tidal currents with time. These currents change not only their velocity but their type of flow as well (Graham and Venno, 1968).

ACKNOWLEDGMENT

I am indebted to Bruce C. Bickford who operated the buoyed and anchored nets in the channel, sometimes during severe weather.

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ABUNDANCE, DISTRIBUTION, MOVEMENTS, AND LENGTHS OF LARVAL HERRING ALONG THE WESTERN COAST OF THE GULF OF MAINE

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ABSTRACT

This paper describes the abundance, distribution, movements, and lengths of larval herring along the western coast of the Gulf of Maine. Larvae were most numerous in the catches throughout the coast in the autumn, reached a low in the winter, and increased in the spring. Growth in the autumn is estimated at 1 to 1.3 mm per 5-day intervals. Larval mortality was highest in the autumn, lower in the winter, and lowest in the spring. The mortality in the winter usually varied with their condition and determined the subsequent level of spring abundance. We selected three different types of estimates as desirable for predicting the recruitment of immature herring to the sardine fishery of Maine: (1) winter mortality, (2) larval condition in the winter, and (3) spring abundance.

The commercial catch of 2-year-old Atlantic herring, *Clupea harengus harengus* Linnaeus, fluctuates annually along the western coast of the Gulf of Maine. The Maine sardine industry processes these immature herring, but cannot anticipate the amount of fish available for canning each year. One approach to this problem is to determine whether the abundance of herring during their first year of life is related to the number of fish entering the fishery. To establish whether such a relationship exists, the desirable estimate of abundance or its correlative must be determined first. We describe the distribution, abundance, movements, and lengths of larval herring along the western coast of the Gulf of Maine. We discuss the seasonal changes in larval abundance caused by their mortality and the relation of the sources of larvae to their distribution and movements. From these analyses we selected three types of estimates: (1) winter mortality, (2) larval condition in the winter, and (3) spring abundance.

Larval herring occur throughout the Gulf of Maine-Georges Bank area. They concentrate in the offshore bank area (Tibbo et al., 1958); along the southeastern coast of Nova Scotia (Das, 1968)[2]; and the western coast of the Gulf of Maine (Graham and Boyar, 1965). During their relatively long larval period, herring may drift with the residual currents about the banks and in the Gulf (Colton and Temple, 1961; Das, 1968, see footnote 2). Racial studies show that these larval herring have three parental stocks; namely, Georges Bank, the southern coast of Nova Scotia, and the western coast of the Gulf of Maine (Anthony and Boyar, 1968; Ridgway, Lewis, and Sherburne, 1969). The relation between the parental stocks and the larvae is not clear.

In the Boothbay area of the Maine coast, herring were found in estuaries and embayments throughout their larval life (Graham and Boyar, 1965). In this area larval catches reached a peak in the autumn shortly after hatching and declined to a minimum during winter. Catches were sporadic in the spring and in May the fish metamorphosed. Evidence that in the spring the larger larvae avoided our conventional sampling gear (Gulf III and meter nets) led to the development of the Boothbay Depressor trawl (Graham and Vaughan, 1966) and buoyed and

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anchored tidal nets (Graham and Venno, 1968). Catches with this gear provided information on mortality in an estuary (Graham and Davis, 1971), condition (Chenoweth, 1970), and seasonal feeding (Sherman and Honey, 1971). Coastal salinity, temperature, and currents were measured during zooplankton surveys (Sherman, 1970) and hydrographic surveys (Graham, 1970a, b).

MATERIALS AND METHODS

Larval herring were sampled in two areas (Figure 1): A coastal area which extended from the headlands to 20 km offshore (50-fm isobath) along the coast from Cape Ann, Mass., to Machias Bay, Maine; and the Boothbay area which extended to 6.5 km offshore (lat 43°45'N) and was bounded by the Sheepscot and Damariscotta estuaries. Collections were made once or twice each season in the coastal area from autumn 1962 through spring 1967; and every other week in the Boothbay area from autumn 1964 through spring 1967. Additional collections, obtained after 1967, will be cited when pertinent. There were 21 stations in the coastal area until the spring of 1965 when the number was increased to 46 to provide more adequate data. In autumn 1966, the area was divided into 30-min squares of latitude and longitude and the squares subdivided into quarters. The 46 quarters sampled on a given cruise were selected randomly. An exploratory winter cruise (1964) was made within the coastal bays and estuaries and two cruises were made in the Boothbay area in early March of 1964 and 1965. In the Boothbay area, samples were obtained in all locations that were navigable for the 13-m vessel, MV *Phalarope*.

Larval herring were collected by the methods listed in Table 1. We captured small larvae in the autumn with a Gulf III sampler (Gehringer and Aron, 1968) and larger larvae in the winter and spring with Boothbay Depressor trawls (Graham and Vaughan, 1966). Catches ob-

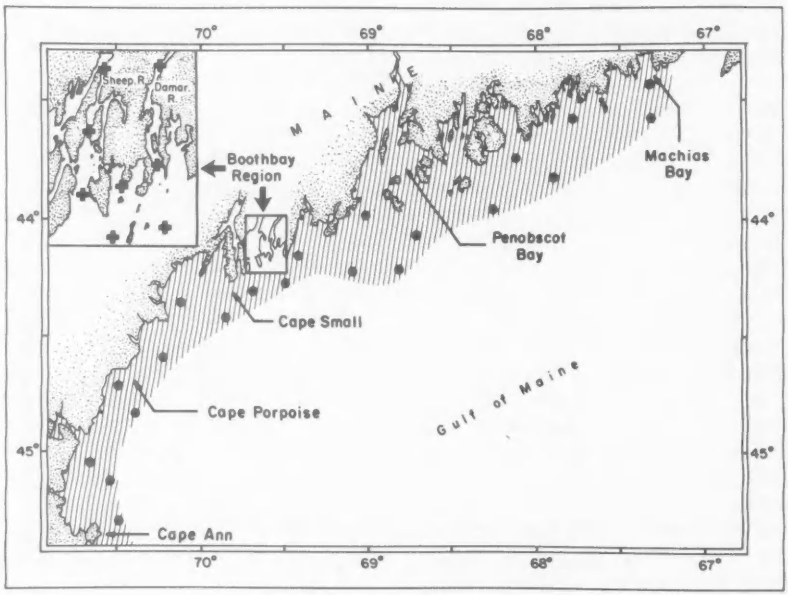

FIGURE 1.—The coastal (hatched) and Boothbay (enclosed) sampling areas along the western coast of the Gulf of Maine. Dots and crosses are station positions; S and D indicate the Sheepscot and Damariscotta estuaries.

TABLE 1.—Methods of sampling larval herring in the western Gulf of Maine, 1962-67. Volume sampled in 7½-min tow = given volume ÷ 4.

Area	Stations	Season	Gear type	Tow		Water strained	Towing velocity
				Depth	Duration		
				m	*min*	m^3	*knots*
Coastal	21-48	Autumn	Gulf III	0-10-20	30	200	6
		Winter-spring	Boothbay Depressor trawl				
			No. 1	0-10-20	30 (or 7½)	4,200 (1,050)	6
			No. 2	0-10-20	30	17,000	4½
			No. 4	0-10-20	30 (or 7½)	8,000 (2,000)	5
Inshore	8	Autumn	Gulf III	0-mid-depth-bottom	30	135	4½
		Winter-spring	Boothbay Depressor trawl				
			No. 1	0-mid-depth-bottom	30	[1]2,800-4,200	4

[1] Dependent on mouth opening of liner.

tained were adjusted to the number of larvae captured per 100 m^3 of water strained during a tow. During the coastal cruises the gear was towed obliquely for 30 min at each station (10 min each at the surface, at 10 m, and at 20 m) except on the coastal cruises after autumn 1966, when each of the 46 quarters was sampled with two oblique 7½-min tows (2½ min at the surface, at 10 m, and at 20 m). The direction of these two tows was selected randomly and catches were averaged to obtain an estimate of abundance. Filtration efficiencies of the sampling gear approached 100%. Comparisons between catch rates of the Gulf III and the Boothbay Depressor trawl differed on individual stations during tests covering the period of their exchange within the sampling program. However, the catch rates were similar for the two gear when they were averaged for stations or for an entire cruise. Experiments also showed differences in catch rates between short and long tows, between tows of different depths, and between tows made during nighttime and daytime. Only the differences between rates during nighttime and daytime were sufficiently important to the analyses of this report and they are given. Information on the length and depth of tow and comparisons of catch rates between the two gear are being prepared for publication.

Larval herring, preserved in 10% Formalin, were measured from the tip of the jaw to the end of the caudal peduncle (standard length). Conversion of this measurement (SL) extended to total length (tip of jaw to the tip of the longest lobe of the caudal fin) (TL) may be made for larvae from 20 to 45 mm SL by:

$$TL = -3.47 + 1.24\ SL$$

RESULTS

HATCHING

Catches of recently hatched herring (4-9 mm) provide evidence that there are several spawning areas along the western coast of the Gulf of Maine, but that the time of hatching differs between the eastern and western sectors of the coast. Recently hatched larvae were captured throughout the coastal sampling area from late September until early November. Some of these larvae had yolk sacs, especially those obtained near the headlands of the Boothbay area, where the occurrence of hatching was monitored each year. Relatively large numbers of larvae were captured east of Cape Small in the early autumn and to the west of this Cape in late autumn (Table 2). The autumnal hatch along the coast was expected, since Boyar (1968) found that the gonads of most adult coastal herring reached spawning condition by late September in this area. Also Goode (1884) and Bigelow and Welsh

TABLE 2.—Coastal distribution of the number of recently hatched larval herring from late September to mid-October and from then to early November; water tempertaures are from mid-October.

Area (Figure 1)	Percentage of larvae, 4-9 mm		Mean temperature (°C) mid-October 1963	
	Sept.-Oct. 1962-63 (N = 267)	Oct.-Nov. 1962-66 (N = 1,872)	Surface	Bottom
Cape Ann-Cape Small	9	97	12	8
Cape Small-Penobscot Bay	54	2	11	9
Penobscot Bay-Machias Bay	37	1	9	10

(1925) reported that herring spawned in the western area later than in the eastern sector of the coast. Hatching of larvae in the spring was observed only once; three larvae (8-9 mm) were captured in the Boothbay area in May.

The earlier hatching in the eastern sector of the coast may be attributed to the distribution of water temperature. The average surface temperature from 1963 through 1965 was 9.1°C in the western sector of the coast and 6.2°C in the eastern sector. Bottom temperatures during the same period averaged 4.5°C in the western sector and 5.6°C in the eastern. Each year the surface water was 2° to 3.5°C warmer in the western than in the eastern sector, while the eastern bottom water was 1° to 1.5°C warmer than in the western sector. These temperature trends were established primarily in the summer (Graham, 1970a) and persisted into the autumn (Table 2). Possibly, cooler autumn surface temperatures in the eastern sector would initiate spawning sooner than in the western sector; warmer bottom temperatures would incubate the eggs faster (Das, 1968, see footnote 2).

SEASONAL ABUNDANCE, DISTRIBUTION AND MOVEMENTS

Larvae were most numerous in the catches throughout the coast in the autumn, reached a low in the winter, and increased slightly in the spring (Figure 2). Catches were largest in the eastern sector of the coast in early autumn, but larger in the western sector by mid-autumn. By late autumn, catches dropped drastically in both sectors and reached a common level throughout the coast. In the Boothbay area the numbers of

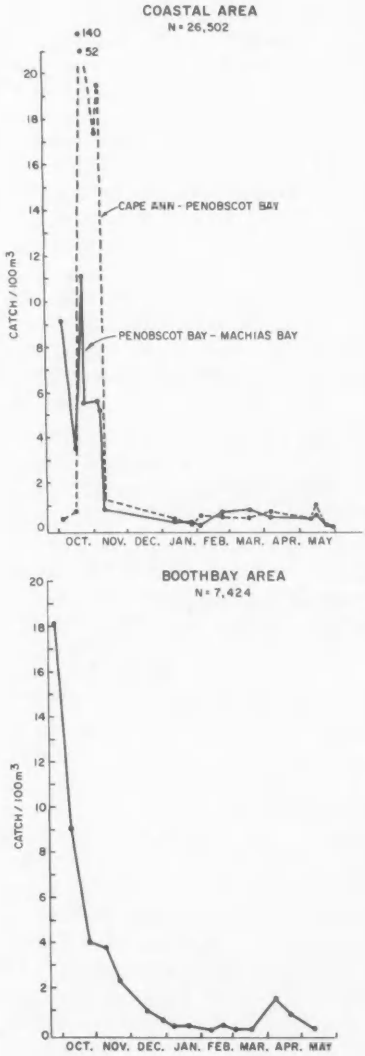

FIGURE 2.—Upper panel - mean catch rates of larval herring in the western (Cape Ann-Penobscot Bay) and eastern (Penobscot Bay-Machias Bay) sectors of the coast during cruises from 1962-67. Lower panel - mean catch rates from the Boothbay area for semimonthly periods combined for the years 1964-67. Points are plotted at the midpoint of the cruise periods.

captured larvae were also highest in the autumn, lowest in the winter with an increase in the spring. The timing of autumnal abundance varied between years and will be discussed in detail in the section on movements. As recorded by Graham and Boyar (1965) the Sheepscot estuary usually contained more larvae than the Damariscotta estuary. About 60-68% of the total catch was taken in the Sheepscot in a given year.

Seasonal changes in the dispersal of larvae were analogous to those of abundance. Larvae were aggregated in the autumn and spring and dispersed in the winter. For instance, catches during an autumn cruise had a coefficient of variation of 214%, during a winter cruise 17%, and during a spring cruise, 50%. Exploratory cruises showed that larvae were dispersed from the headlands to 28 km up the estuaries in the Boothbay area during early March when winter conditions still prevailed.

Changes in distribution occurred in the autumn and spring when the larvae moved landward. These changes were apparent when the average catch rates from the Boothbay area ($\bar{x}$ Boothbay) were compared synoptically with those from cruises in the adjacent coastal area from Cape Small to Penobscot Bay ($\bar{x}$ coastal). The synoptic catch rate from the Boothbay area was obtained by interpolating between rates of the biweekly cruises that occurred a few days before and after a given coastal cruise. The percentage catch rate of larvae in the Boothbay area [$\bar{x}$ Boothbay/$\bar{x}$ Boothbay + $\bar{x}$ coastal)] $\times$ 100 did not exceed 40% during October when hatching was at its peak, then reached almost 90% in November coincident with a decline in hatching (Figure 3). The percentage was again low in February and March, but increased to about 85% in April and May prior to metamorphosis. Similar comparisons between Boothbay data and those from coastal areas east and west of Boothbay did not yield these relations. Apparently, the shoreward shift in distribution was not synchronized along the entire coast.

Other movements of larvae were evident from an analysis of the data from the coastal and Boothbay areas. In autumn, an alongshore movement from east to west was apparent when

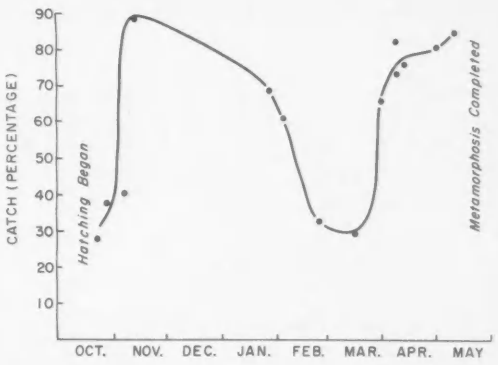

FIGURE 3.—The change in percentage in the average catch rate in the Boothbay area as compared with the average catch rate in the coastal area.

larvae were obtained in the Boothbay area that were larger than those recently hatched in the western coastal sector. The movement of larvae in the spring was marked by their accumulations in locations receiving shoreward intrusions of coastal water and by the relation of their distribution with that of surface salinity. The intrusions resulted from eddies formed by the spacing of river discharge along the western sector of the coast (feathered arrows, Figure 4). The configurations of isohalines and lines of equal larval density throughout the coast were often similar. Such similarity indicated that the magnitude of station-to-station differences in catch paralleled the station-to-station differences in salinity. These differences were accumulated for coastal stations from west to east and their frequency distributions were plotted on probability paper for two cruises having widely different salinity distributions (Figure 5). The cumulative frequencies of salinity and catch were alike for a given cruise, but differed between cruises. We infer from these results that the larvae are carried by currents, indicated by the station-to-station differences in salinity. The precise direction of drift cannot be ascertained because it is not possible to determine whether the salinity distribution is causing the current or is the effect of the current, perhaps generated by winds.

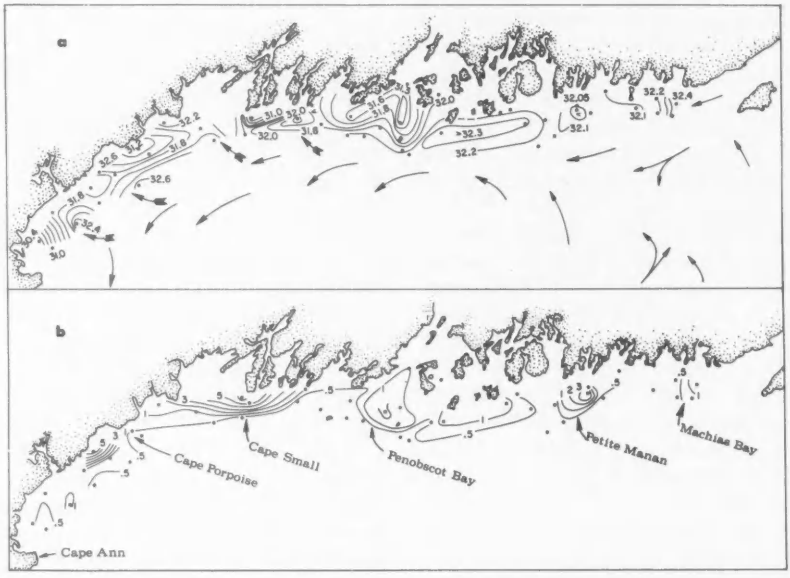

FIGURE 4.—(a) Isohalines (‰) during a spring cruise, March 28-April 13, 1967. Feathered arrows indicate shoreward intrusions of coastal water (from Graham, 1970b), and unfeathered arrows indicate current directions along the coast (from Bumpus and Lauzier, 1965). (b) Isolines of larval catch rates (no/100 m³) for the above cruise.

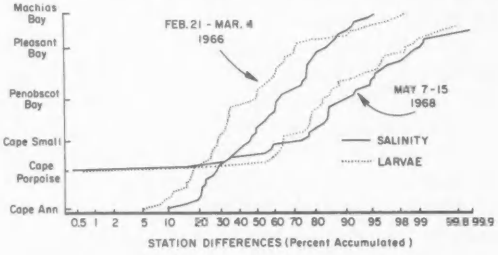

FIGURE 5.—Accumulated frequency distributions of station-to-station differences from west to east along the coast. The cruise in 1968 began to the east of that in 1966.

Larval movements up the estuaries during autumn were easier to detect in the Boothbay area because larvae were transported inshore primarily by tidal flows (Graham and Davis, 1971). Tidal flows followed the inshore-offshore axes of the estuaries and embayments; thus the landward movement was detected by grouping catches made at the three outer estuarine, three lower estuarine, and two upper estuarine stations, and plotting them in a time series. Peaks in larval abundance progressed from outer to upper estuarine stations with time, suggesting an inshore movement of the larvae (A, B, and C in Figure 6). Two such progressions were obtained in 1966 and one in both 1964 and 1965. In 1964, larvae passed the outer and lower stations between our scheduled cruises and appeared first at the upper stations as a peak in abundance in early October. In spring, larvae were always more abundant at the upper estuarine stations, and progressions in peaks of abundance up the estuary were not apparent.

LARVAL LENGTHS

The rate of increase in average length varied seasonally and geographically. Data from the coastal and Boothbay areas showed a marked

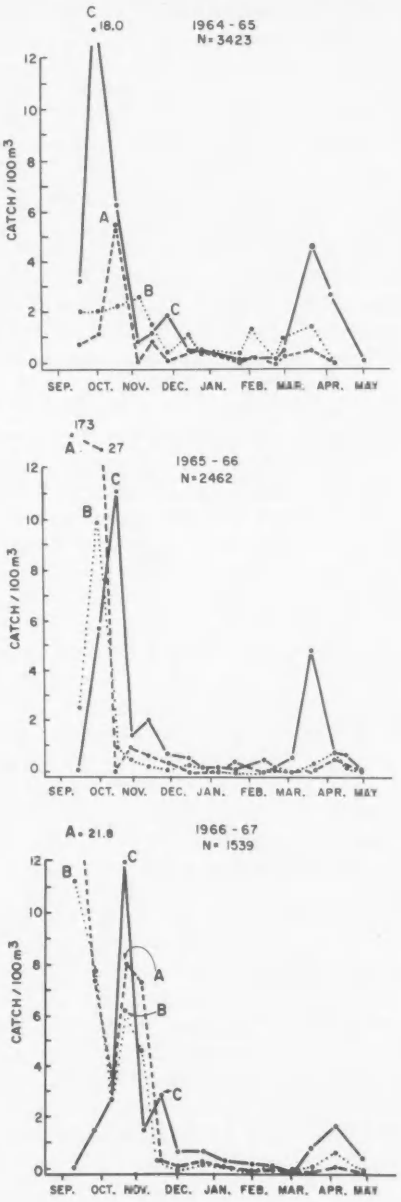

FIGURE 6.—Seasonal changes in larval abundance in the Boothbay area during 1964-67. Values are plotted for outer (A), lower (B), and upper estuarine (C) stations.

increase in length in the autumn followed by a more gradual increase in the winter and spring (Figure 7). During the autumn and spring the increase in length accompanied a comparable increase in weight, but not in the winter when the larvae were very thin (Chenoweth, 1970). In the coastal area the increase in length

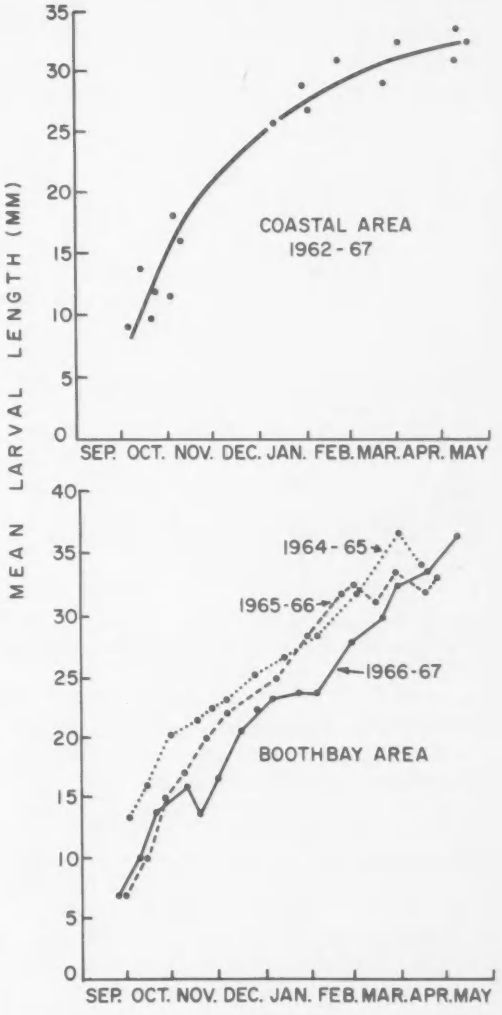

FIGURE 7.—Seasonal change of mean larval length in the Boothbay and coastal areas, 1962-67.

appeared asymptotic while the average length fluctuated above and below 32 mm in the Boothbay area from March through May in 1965 and 1966. Differences in the average length also occurred between the eastern and western sectors of the coast. In late September to mid-October, the mean lengths did not differ greatly along the coast (Figure 8). By early November the mean length was larger in the eastern sector than in the western sector, but this difference diminished in winter; by spring mean lengths were similar along the coast.

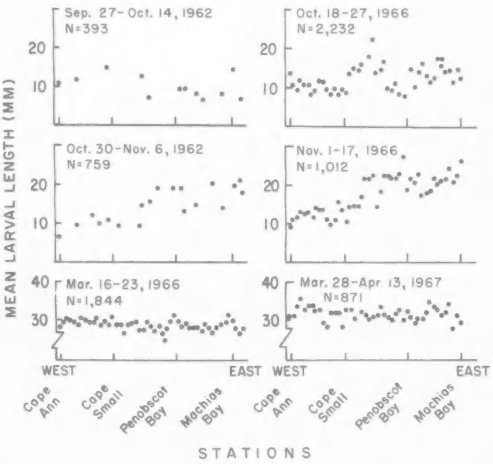

FIGURE 8.—Variations in the average length of larval herring from west to east along western coast of the Gulf of Maine.

The seasonal change in mean length (Figure 7) was influenced by the movements of larvae, their avoidance of our sampling gear, and their departure from the vicinity of our sampling stations after metamorphosis. Broods of larval herring moved shoreward in the autumn from the coastal water, but the size at which they initially entered the Boothbay area varied. This is illustrated by data from 1964 and 1965; data from 1966 were similar to those of 1965. In autumn 1964, two broods of larvae (labeled a and b in Figure 9) initially entered the Boothbay area; the more abundant had a size mode of 13 mm, the other was recently hatched and had a size mode of 9 mm. By mid-October these two broods were of equal abundance. In November a third brood (c) was detected, during a coastal cruise, that had a modal length of 13 mm, equal to the modal length of larvae initially entering the Boothbay area. Presumably, the addition of this group in part slowed the shift in modal length to only 3 mm from mid-November to late December. These variations in size resulted from the location of the Boothbay area within an east-west coastal zone of transition for hatching time. Also, some of the larvae hatched in the eastern sector of the coast at an earlier time and were carried westward along the prevailing currents (Graham, 1970b) and then into the Boothbay area.

In autumn 1965, a single brood (d) of recently hatched larvae with a modal length of 7 mm initially entered the area. In October, this brood was still the most important contributor to the inshore area, since the modal size from a coastal cruise in October coincided with the seasonal progression of larval size within the Boothbay area. A second group (e) of recently hatched larvae entered the area in early November.

In the spring it was obvious that we were failing to catch the larger larvae and the spring peak in catch rates should have been considerably larger than that recorded for daytime tows. We assumed that this failure was due to their avoidance of our gear because we captured more of these larger larvae at night when they could not see the gear. Day and night cruises were alternated in the Boothbay area from January through April during 1965 and 1966. The size ranges of larvae captured during these cruises were the same, but the modal length was much larger for larvae captured during the night cruises. The length-frequency curves for all larvae from the day and night cruises showed two distinct modes, one at 33 mm and the other at 40 mm (Figure 10). At 36 mm the percentages of larvae in the day and night catches were identical. For larvae larger than 36 mm the percentages increased for night catches and decreased for day catches, indicating that avoidance increased progressively until the larvae grew to 40 mm. Initial nighttime catches of

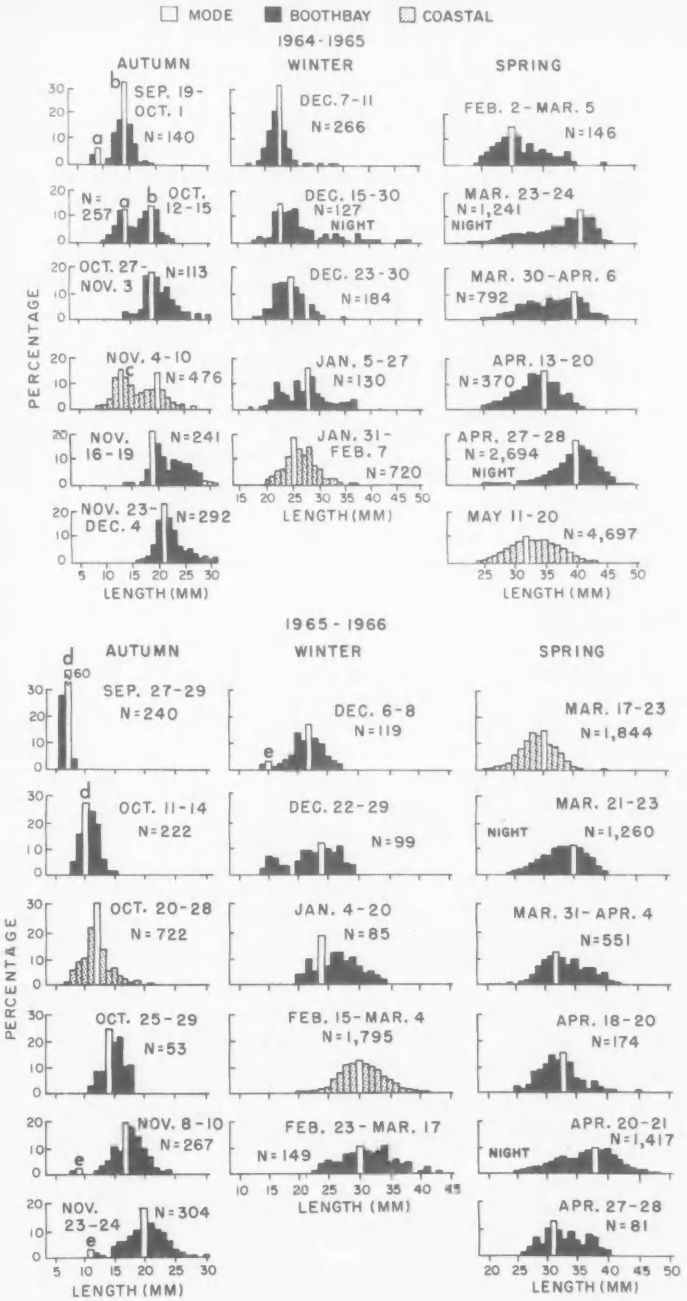

FIGURE 9.—Size distribution of larval herring during 1964-66. Only the most obvious modal lengths are indicated for the data from the Boothbay and coastal areas and those modes discussed in the text are labeled a to e.

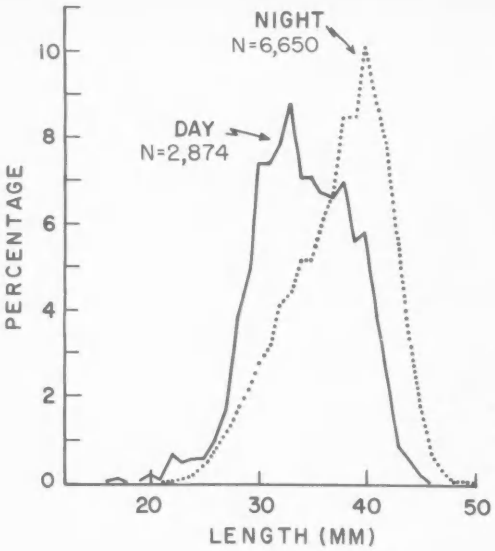

FIGURE 10.—Length-frequency curves of larvae captured in the Boothbay area at night and during the day.

those larvae larger than 36 mm occurred earlier in the year and their peak in abundance occurred later than that of larvae captured during the day (Figure 11). In 1964, losses by avoidance began in December. Failure to catch larvae began later the following year (in January) because the larvae that initially entered the Boothbay area were smaller than those that entered in 1964 (Figure 7). Catches of larvae larger than 36 mm in length in the Boothbay area were similar to those obtained with buoyed and anchored nets set in the Sheepscot estuary at night during 1966. This similarity indicated the ease with which larvae were captured at night. The buoyed nets strain water at a much lower velocity than the trawl.

In late April larvae were occasionally observed schooled in shallow coves. By late May large numbers of these fish were frequently observed in the shallow coves whereas the numbers captured at our sampling stations had declined. This change in distribution was coincident with the period of metamorphosis (about 41-50 mm SL) from larval to juvenile form. Metamorphosed herring were found in the Boothbay and other inshore areas but not in the outer coastal waters during the summer (Davis and Graham, 1970).

Variations in the lengths of larvae in our samples related to their shoreward movements, avoidance of gear, and departure from our sampling stations, caused discrepancies when estimating the real growth of larvae in their environment. Some estimate of growth rate may be obtained, however, from changes in modal length at certain times of the year. During 1965, the modal lengths of a single abundant group of larvae may be traced from the autumn into December. This group was not greatly influenced by mixing with other groups of different sizes and avoidance of our gear was not yet important. From late September to early December, the

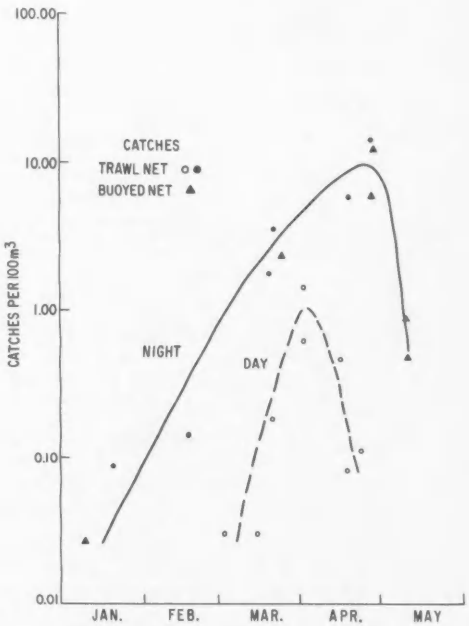

FIGURE 11.—Monthly progression of larval catches (larvae 36 mm and larger) in the Boothbay area from trawl tows at night and during the day and in the upper Sheepscot estuary from buoyed and anchored nets at night.

larvae appeared to grow about 1 mm every 5 days. Similarly, in 1964 modal lengths may be traced from late September to early November with an apparent larval growth of 1.3 mm every 5 days, but then the mode became difficult to identify.

DISCUSSION

SEASONAL CHANGES IN ABUNDANCE AND LARVAL LENGTH CAUSED BY MORTALITY

After larvae hatched and accumulated in the coastal bays and estuaries, their abundance was determined by the rate at which they died. The autumn mortality was especially severe, for the catch declined in the Boothbay area (Figure 6) despite the addition of successive broods to the area throughout the autumn. This high mortality was also indicated by the failure of length modes to persist into the winter. The number of larvae in a given mode apparently was reduced with time and coincidently with differential growth until the larvae were too sparse in the catches to form a distinguishable mode. In 1966 the disappearance of a mode of relatively large fish from the catch caused a sharp drop in the mean larval length during November (Figure 7). Although the mean length increased either with subsequent growth of the remaining larvae or with the addition of larvae to the area, it remained below the mean lengths of the other years throughout the winter. Winter mortalities were not as high as those in the autumn. Graham and Davis (1971) determined mortalities from December to January for larvae captured in the Sheepscot estuary during 1964-67 and recently for mortalities for 1968-69. Estimates for the 6 years varied from 22% to 52% for 15-day intervals and appeared statistically reliable with the largest spread in the 0.95 fiducial interval in 1968 (27.7-36.9%), and the smallest in 1966 (22.0-22.8%).

Extensive reductions in our catch rates in the late spring occurred from avoidance of the gear by the larvae and their departure from our sampling stations. Catches at the upper estuarine stations in the Boothbay area were larger than those at the lower and outer stations. Progressive peaks in abundance, that were present in the autumn, were absent from outer to upper estuarine stations in the spring. One explanation for the lack of progression is that the larger larvae moved landward so rapidly as to be undetected in the spring. Another and more likely explanation is that their mortality was sufficiently low to permit an accumulation of larvae at the landward extremity of their movement where numbers always greatly exceeded the number of larvae moving into the area.

Estimates of annual mortality were based on winter mortality (Graham and Davis, 1971) because measurements of total mortality during a given year were impracticable as they were influenced by larval movement in the autumn and in the spring. For most year classes, a higher winter mortality recorded in the upper end of the Sheepscot estuary coincided with a smaller maximum catch there in the subsequent spring. Also, higher winter mortalities usually coincided with a poorer condition or well-being of the larvae (Chenoweth, 1970) for the Boothbay area (Figure 12).

The causes of larval mortality along the western coast of the Gulf of Maine were not determined, but inferences were made by Chenoweth (1970) and by Sherman and Honey (1971). Essentially, they suggested that winter mortality might be related to lower lethal temperatures, inhibition of feeding by low temperatures, and a scarcity of food. Sherman (personal communication) found in recent studies that the larval guts were frequently occluded by parasites, which may cause death.

SEASONAL CHANGES IN DISTRIBUTION RELATED TO LARVAL SOURCES

After hatching, the larvae shifted their distribution from spawning areas to the coastal bays and estuaries. These destinations were apparent from our catches, but not all the sources or spawning areas were determined. The sources of larval herring in the Gulf of Maine, including the western coast, their movements from these

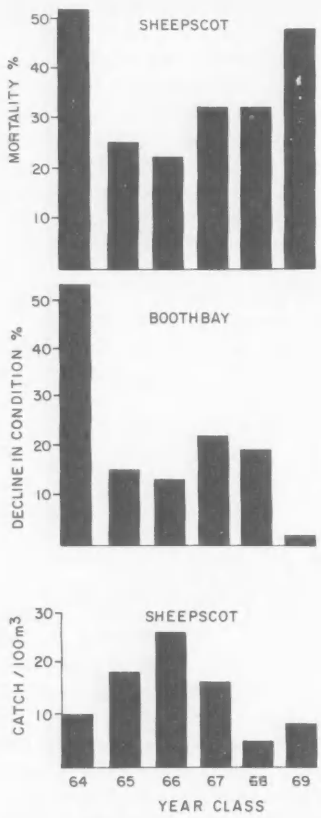

FIGURE 12.—A comparison among year classes of winter mortality of larvae in the Sheepscot estuary (upper panel), the decline in condition of larvae in the Boothbay area (center panel), and the subsequent spring catch rates in the Sheepscot (lower panel).

sources, and the resulting changes in their distributions have received attention from other investigators.

Spawning grounds of herring were located in the past by surveying the distribution of recently hatched larvae (Tibbo et al., 1958), and more recently by collecting eggs off the spawning grounds (Noskov and Zinkevich, 1967). Migrations of larvae from these grounds were traced by assuming that they were transported similarly to a particle of water. Thus, their paths of migration from the grounds were located within the residual currents at the surface. Boyar et al. (1971) reviewed such evidence for the Georges Bank-Gulf of Maine area and decided that larvae may enter the eastern sector of our sampling area from the spawning grounds off southwestern Nova Scotia, and that some larvae from Nova Scotia may be carried along the coast of Maine as far as Cape Cod, Mass. In a concurrent paper, Iles (1971) reported on the dispersion of larvae from southwest Nova Scotia and concluded from his data that the larvae were transported into the Bay of Fundy where they were retained during the winter. Boyar et al. (1971) also suggested that larvae entered the western sector of our coast from Jeffreys Ledge, Cashes Ledge, Stellwagen Bank, and other areas collectively just offshore of the coastal sector.

The larvae from these two sources, Nova Scotia and the ledges and banks in the southwestern Gulf of Maine, possibly contributed to the coastal larval population in the spring. Such a contribution would partially explain the high catch rates obtained in the Boothbay area where larvae accumulated in the autumn and spring. The autumnal movements of larvae into the area subsided by early December. The catch in the area at that time was less than the peak catch obtained in the subsequent spring, indicating that larvae present in autumn could not account for all of the larvae found in the same area in the spring. Much of the spring catch, therefore, may be formed by emigrants. Das (1968, see footnote 2) also discovered a similar emigration by examining length-frequency distributions of larvae in the coastal area of southwest Nova Scotia. And Sameoto (1971)[3] reached a similar conclusion from catches of larval herring entering St. Margaret Bay on the southeastern coast of Nova Scotia.

Another explanation for the differences in the early winter and the spring catches in our sam-

[3] Sameoto, D. D. 1971. The distribution of herring (*Clupea harengus L.*) larvae along the southern coast of Nova Scotia with some observations on the ecology of herring larvae and the biomass of macrozooplankton on the Scotian Shelf. Fish. Res. Board Can., Tech. Rep. 252, 72 p.

pling areas may be deduced from the residual surface currents. In winter, the direction of these currents is usually offshore; in spring, the currents are often directed inshore. Thus, larvae swept offshore in the winter might be returned to the coast in the spring. However, we did not detect any concerted movement by the larvae offshore in the winter and suspect that the assumption that larvae are transported similarly to a particle of water is often an oversimplification. The factors controlling the movement and retention of the larvae in shoal water must be investigated to understand the possibilities of their transport.

ANNUAL CHANGES IN ABUNDANCE AND THE FISHERY

The goal of this research was to choose an estimate of larval abundance or its correlate that could be used to predict the annual recruitment of immature 2-year-old herring to the sardine fishery of the western coast of the Gulf of Maine. Three different types of estimates were chosen: (1) winter mortality, (2) condition in the winter, and (3) maximum abundance in the spring. Sampling should continue over a number of years to determine whether the relations between the three measures have substance and whether any one or all of them are pertinent to predicting the abundance of 2-year-old herring.

A tentative comparison between the percentage of 2-year-old fish taken in the fishery with the percentage of winter mortality of the corresponding year class during 1964-68 is shown in Figure 13. Years of low mortality were usually related to subsequent greater percentage of 2-year-old fish in the fishery.

Estimates of winter condition are important because they provide an insight as to the cause of larval mortality. Because winter condition correlates with winter mortality, larval deaths are probably caused by debilitating factors such as disease, starvation, or parasitism. But, lack of agreement during 1969 (Figure 12) would involve other factors as well, such as predation or sudden and transient effects of man's activities within the coastal environment.

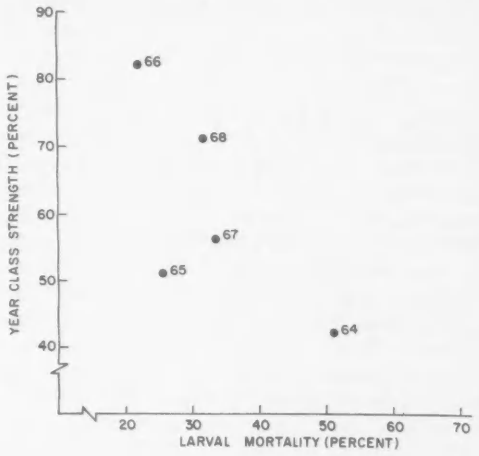

FIGURE 13.—Comparison between the percentage of 2-year-old herring captured in the Maine sardine fishery and the winter larval mortality for a given year class. Age composition of the fishery was determined by John E. Watson (personal communication). The catch also includes fish from the adjacent Canadian coast.

Estimates of abundance in the spring are necessary as well as winter mortality estimates because the number of larvae surviving until spring theoretically depends upon the initial number of larvae present by the end of autumn. During each of the years in which winter mortality was estimated in this study, the autumnal abundance was reduced to approximately the same level by early winter. During years of very successful hatching, the autumn mortality might not be sufficient to reduce the number of larvae to a level common to that of previous years. The subsequent spring abundance would then be determined by the initial number of larvae present in early winter as well as the winter mortality. The estimates of spring abundance in the Boothbay area and in the coastal area between Cape Small and Penobscot Bay (Figure 14) did not agree with the estimates obtained with buoyed and anchored nets in the Sheepscot for year classes 1964-65 (Figure 12, bottom panel). We do not understand the reason for this difference.

To date, monitoring of the winter mortality

and condition and spring abundance of larvae has been largely confined to the Boothbay area; the possibility of extending monitoring to other areas of the coast is being investigated. Nevertheless, events in the ecology of the larvae in the Boothbay area could represent those of the entire coast of the Gulf. Seasonal changes in larval abundance are similar along the coast and are comparable to those in the coastal area off southwest Nova Scotia (Das, 1968, see footnote 2) and on Georges Bank (Boyar et al., 1971). Yearly changes in oceanic conditions along the coast and in the offshore Gulf of Maine are also related (Colton, 1968). Further correlation between ecological events in the Boothbay area and those in other areas of the Gulf, at least adjacent areas, is evidenced by the agreement of the winter mortality estimates obtained in the Sheepscot and the subsequent spring abundance there. Larvae captured in the spring include emigrants from areas other than Boothbay. Correct forecasts of a poor fishery, to date, coincided with poor recruitment to the fishery; unfortunately, forecasts have not been made during years of good recruitment in the western sector.

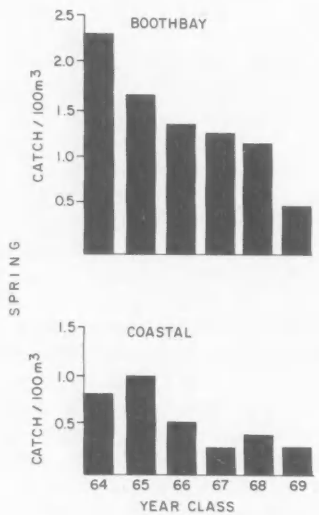

FIGURE 14.—Peak catches for larval herring in the spring among year classes 1964-69; in the coastal area between Cape Small and Penobscot Bay and in the Boothbay area.

SUMMARY OF ABUNDANCE AND DISTRIBUTION

The abundance and distribution of larval herring along the western coast of the Gulf of Maine is determined by their movements and mortality. Two inshore movements, one in the autumn and the second in the spring, are separated by a period of larval dispersal. Larvae hatch along the coast in autumn and penetrate the bays and estuaries. Their inshore movement decreases by early winter and in midwinter they disperse; at this time concentrations of larvae are infrequent inshore and along the coast. A second shoreward movement begins with the advent of spring. Larvae which hatched the previous autumn along the coast, and probably some which hatched beyond our sampling area, aggregate when making this shoreward movement. The inshore movement is completed by the end of spring when the majority of the larvae have assumed their adult form.

Mortality during the inshore movement in the autumn is very high. Although it is lower in the winter, mortality during this season may determine the abundance of larvae in the spring because the numbers are reduced by early winter to a relatively common level each year. The lower winter mortality may be related to the dispersal of the often weakened larvae; dispersal would reduce intraspecific competition for food and space. The lowest mortality occurs in the spring when the larvae are in good condition as shown by their ability to avoid high-speed trawls with large mouth openings.

The movement of the larvae shoreward within the complex currents of the coast is a striking feature of their coastal ecology.

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AN ECOLOGICAL STUDY OF GEORGIA COASTAL FISHES

MICHAEL D. DAHLBERG[1]

ABSTRACT

The distribution of fishes in relation to ecological factors was studied in a Georgia estuary and adjoining beach and coastal plain creek waters to establish fundamental base lines for the ecology of a relatively undisturbed section of the coast. The distributions of 168 fish species were related to nine recognizable habitats, temperature, and salinity. Length frequencies and spawning seasons were determined for most of the trawled species that contributed significantly to fish production in the estuary.

Collecting by a variety of techniques permitted evaluations of types of life cycles, of diversity in the various aquatic habitats, and of distribution patterns within the estuarine complex and adjoining waters. Numbers of species collected in nine aquatic habitats were as follows: beach - 114, lower reach of the estuary - 100, high marsh - 56, upper and middle reaches - 61, oligohaline creek - 40, fresh water - 39, tidal canal - 22, low-salinity tidal pool - 22, high-salinity tidal pool - 37.

Estuaries are highly productive and support important sport and commercial fisheries. A majority of the nation's commercial finfish and shellfish species and many coastal sport fishes utilize the estuarine environment during at least part of their life cycle. Estuaries are important recreational areas, especially for fishing, partly because of their proximity to civilization. Unfortunately, this proximity and lack of pollution controls have resulted in mass degradation of the nation's estuaries through pollution, filling, and dredging. Pre-pollution studies are essential for the precise evaluation of the ecological impact of stresses on estuaries. The normal functioning of estuaries must be understood before scientists can evaluate the effects of various stresses on estuaries. There is an urgent need to determine the significance of coastal habitats to the various life history stages of coastal fishes. The central Georgia coast presents an opportunity to study the ecology of fishes in a relatively undisturbed estuary and establish fundamental base lines for the detection and evaluation of pollution. Aspects of fish ecology that have been selected for examination include (1) distribution of fishes in relation to recognizable habitats, salinity, and temperature, (2) size frequencies and spawning seasons of many abundant species, (3) diversity of fishes in each of nine habitats, and (4) types of life cycles.

Except for the Brunswick and Savannah regions, Georgia estuaries are relatively free of pollution. However, certain Golden Isles along the Georgia coast are being considered for strip mining for titanium and phosphate. A nuclear power plant is under construction on the lower Altamaha River. Recent developments in the estuary studied herein include a kraft paper mill, a shrimp culture farm that may not be completed, and an interstate highway that may alter tidal flushing.

A complete picture of species distributions and size in coastal waters can be obtained only if all major habitat types are examined (Springer and Woodburn, 1960). Extensive trawling and seining were undertaken to achieve this goal. Comparisons with other studies are complicated by the difference in types and numbers of habitats sampled and differences in collecting methods.

There has been little work on the ecology of fishes of the U.S. Atlantic coast between Cape Hatteras, N.C., and northern Florida. Tagatz (1968) surveyed the fishes of St. Johns River,

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Fla. Tagatz and Dudley (1961) studied the seasonality of fishes in four coastal habitats near Beaufort, N.C. In South Carolina, Bearden (1961) published a field guide to the common marine fishes, compiled an unpublished list (1961) of marine fishes, and surveyed the elasmobranchs (Bearden, 1965). Lunz and Schwartz (1970) published an 18-year study of South Carolina coastal fishes.

Anderson (1968) surveyed the fishes caught by shrimp trawling from South Carolina to northeastern Florida from 1931 to 1935. His data are not tabulated here because many species complexes were identified only to genus and his collections were from regions other than the estuary under study. Miller and Jorgenson (1969) studied the seasonal abundance and length frequencies of fishes collected by seining at a beach habitat on St. Simons Island and at two high marsh stations, one near Jekyll Island and one near Meridian, Ga. They also listed the fishes collected at a freshwater station in the Altamaha River. Dahlberg and Heard (1969) surveyed the common elasmobranchs of the Georgia coast. Dahlberg and Odum (1970) demonstrated the trawl diversity of Georgia estuarine fishes collected over 14 months. Dahlberg (1971a)[2] presented an annotated list of the Georgia estuarine and coastal fishes. A section of an unpublished ecological survey (Dahlberg, 1971b)[3] was the basis for this report.

LOCATION AND DESCRIPTIONS OF HABITATS

Composition and diversity of fish species in nine aquatic habitats along the Georgia coast are compared in this study. Salinity, temperature, and some aquatic plants and animals that are characteristic of these habitats are given in Table 1.

[2] Dahlberg, M. D. 1971a. An annotated list of Georgia coastal fishes. *In* An ecological survey of the coastal region of Georgia, p. 255-300. Unpublished report to National Park Service from University of Georgia Institute of Natural Resources, Athens.

[3] Dahlberg, M. D. 1971b. Habitat and diversity of the fishes in North and South Newport Rivers and adjacent waters. *In* An ecological survey of the North and South Newport Rivers and adjacent waters with respect to possible effects of treated kraft mill effluent, p. 36-121. Unpublished report to Georgia Water Quality Control Board from University of Georgia Marine Institute, Sapelo Island.

TABLE 1.—Salinity, temperature, characteristic plants and animals of habitats studied, exclusive of freshwater creek habitat.

Sapelo Island Beach

Salinity—Range was 25.0 to 31.3‰ except when flood waters reduced salinity. Measured at 6.8 to 7.7‰ along south end of beach and 15.2‰ in surf near Big Hole at low tide in April 1970.

Plants—Sea oats *(Uniola paniculata)* are the most conspicuous plant on dunes along the beach.

Invertebrates seined or observed—Ghost crab *(Ocypode quadrata)*, polychaete worm tubes *(Onuphis microcephala*, and *Diopatra cuprea)*, horseshoe crab *(Limulus polyphemus)*, hermit crabs *(Clibanarius vittatus*, and *Pagurus longicarpus)*, gastropods *(Busycon carica*, and *Nassarius)*, sea cucumber *(Thyone briareus)*, sand dollar *(Mellita quinquiesperforata)*, isopod *(Aegothoa oculata)*, white shrimp *(Penaeus setiferus)*, shrimp *(Palaemonetes pugio)*, blue crab *(Callinectes sapidus)*, and squid *(Lolliguncula brevis)*.

Lower Reach of the Estuary - Trawl Stations 1-9, 12-14

Salinity—Averages for these stations ranged from 21.4 to 28.9 ‰ from 1967 to 1970 (Dahlberg et al., 1971, see text footnote 3).

Temperature—Averages for the 12 stations ranged from 8.1° (January) to 31.2°C (August).

Plants—Cord grass *(Spartina alterniflora)* is the dominant plant.

Invertebrates—Commercial species are white shrimp, brown shrimp *(Penaeus aztecus)*, and pink shrimp *(P. duorarum)*, American oyster *(Crassostrea virginica)*, and blue crab. Other common species are too numerous to list here.

High Marsh

Salinity—Generally 15 to 30‰.

Plants—*Spartina alterniflora* and *Juncus roemerianus* are characteristic.

Middle and Upper Reaches

Salinity—Range was 11.7 to 29.0‰ and average was 21.2‰ at lowermost station, trawl station 10. Range was 0.3 to 18.7‰ and average was 5.3‰ at uppermost station (F).

Temperature—Range was 8.3° to 31.7°C and average was 20.9°C at the lowermost station, trawl station 10. Range was 9.0° to 30.0°C and average was 21.5°C at uppermost station, station F.

Aquatic plants—*Spartina alterniflora*, *Juncus roemerianus*, tall cord grass *(Spartina cynosuroides)*, marsh elder *(Iva frutescens)*, bulrush *(Scirpus robustus)*, primrose-willow *(Jussiaea)*.

TABLE 1.—Continued.

Sapelo Island Beach—Cont.

Semiaquatic invertebrates—*Uca pugnax, Sesarma, U. pugilator.*

Aquatic invertebrates that were seined, in decreasing order of abundance—*Palaemonetes pugio,* white shrimp, blue crab, *Palaemonetes vulgaris,* brown shrimp.

Riceboro Creek in vicinity of U.S. Highway 17 (oligohaline)

Salinity—Range was 0 to 13.6‰ and average was 3.0‰ for 1968-70.

Temperature—Range was 3.5° to 30.5°C and average was 21.2°C for 1968-70.

Aquatic plants—*Spartina alterniflora, Juncus roemerianus,* waterwort *(Elatine americana),* spike-rush *(Eleocharis acicularia), Iva frutescens, Spartina cynosuroides,* saw grass *(Cladium jamaicense),* groundsel-tree *(Baccharus halimifolia),* arrowhead *(Sagittaria),* water hemlock *(Cicuta maculata), Jussiaea* sp., *Scirpus robustus, Scirpus* sp., salt grass *(Distichlis spicata),* mock bishop-weed *(Ptilimnium capillaceum),* sedge *(Cyperus virens),* and beak rush *(Rhynchospora* sp.).

Invertebrates of lower Riceboro Creek, in decreasing order of abundance in net collections—*Palaemonetes pugio,* blue crab, white shrimp, *Rhithropanopeus harrisi,* and brown shrimp. Other invertebrates of lower Riceboro Creek, reported in Heard and Heard (1971)[1] and Heard and Sikora (In press) include crabs *(Uca minax,* and *Sesarma cinereum),* amphipods *(Corophium* sp., *Orchestia grillus, O. uhleri, Gammarus tigrinus, Corophium lacustre,* and *Melita nitida),* isopods *(Cyathura polita, Cassidinidea lunifrons, Munna reynoldsi, Sphaeroma destructor,* and *Ligia exotica),* tanaid *(Leptochelia),* barnacle *(Balanus improvisus),* polychaetes *(Namalycastis abiuma,* and *Nereis succinea),* gastropods *(Littoridinops tenuipes, Hydrobia, Detracia floridana,* and *Melampus bidentatus),* clams *(Cyrenoidea floridana,* and *Polymesoda carolinae).*

Tidal canal

Salinity—Range was 0.3 to 23.2‰.

Temperature—Range was 8.0° in February 1968 to 30.1°C in August 1967.

Aquatic plants—*Iva frutescens, Borrichia frutescens, Spartina alterniflora, Juncus roemerianus,* glasswort *(Salicornia virginica),* and *Distichlis spicata.*

Semiaquatic invertebrates—*Uca minax, U. pugilator,* and *Sesarma* sp.

Aquatic invertebrates seined, listed in decreasing order of abundance—*Palaemonetes pugio,* white shrimp, blue crab, and brown shrimp.

Low-salinity tidal pools

Salinity—Range was 0 to 24.4‰.

Temperature—Range was 7.3° (January 1970) to 28.2°C (September 1969).

Marsh plants—*Spartina alterniflora, Juncus roemerianus, Salicornia virginica, Eleocharis* sp., *Bacopa monnieri,* aster *(Aster tenuifolius), Distichlis spicata, Scirpus* sp., and *Iva frutescens.*

Semiaquatic invertebrates—*Uca minax, U. pugilator,* and *Sesarma* sp.

Aquatic invertebrates—*Palaemonetes pugio,* and blue crab (juvenile).

High-salinity tidal pools

Salinity—Range was 14.7 to 34‰ in "east pools" and 13.1 to 30.3‰ in "west pools."

Temperature—Range was 8°C in January and February to 32°C in July, August, and September.

Marsh plants along road bank—*Iva frutescens, Borrichia frutescens, Baccharus halimifolia, B. angustifolia* - false willow.

Marsh plants occurring below road bank in the marsh—*Spartina alterniflora, Juncus roemerianus, Salicornia virginica, Distichlis spicata, Batis maritima,* and *Aster tenuifolius.*

Semiaquatic invertebrates—*Sesarma* sp., *Uca pugnax, U. pugilator,* and *U. minax* (uncommon).

Aquatic invertebrates seined, listed in decreasing order of abundance—*Palaemonetes pugio,* blue crab, white shrimp, and brown shrimp.

[1] Heard, R. W., Jr., and E. J. Heard. 1971. Notes on the natural history and invertebrate fauna of the Upper North Newport River. *In* An ecological survey of the North and South Newport Rivers and adjacent waters with respect to possible effects of treated kraft mill effluent, p. 234-246. Unpublished report to Georgia Water Quality Control Board from University of Georgia Marine Institute, Sapelo Island.

Figure 1 illustrates the estuarine complex that was studied, with the exception of the freshwater and Sapelo Island stations. Figure 2 gives locations of stations in the upper part of the North Newport River and oligohaline region in relation to the paper mill (station G), creeks, marsh, railroad, highway, and proposed expressway.

An estuary ranges from the oligohaline creeks to the sounds and barrier islands. Ocean beaches are generally not considered as part of the estuary even though the outflow from estuaries, at least in Georgia, affects beaches and offshore areas where the highly turbid and productive estuarine waters are visible to several miles offshore. This study attempts to evaluate the ecological importance of the following seven estuarine habitats and adjoining beach and freshwater habitats to coastal fish populations. The habitat divisions are somewhat arbitrary as they are all interrelated parts of a single aquatic ecosystem along the coast.

Habitat 1: Sapelo Island Beach (Figure 3).—This station is the ocean beach on Sapelo Island and is known locally as Nannygoat Beach. This beach extends between Dean Creek at the south end and a lagoon (Big Hole) that separates the north end of this beach from Cabretta Island. Most samples were taken in the surf zone near

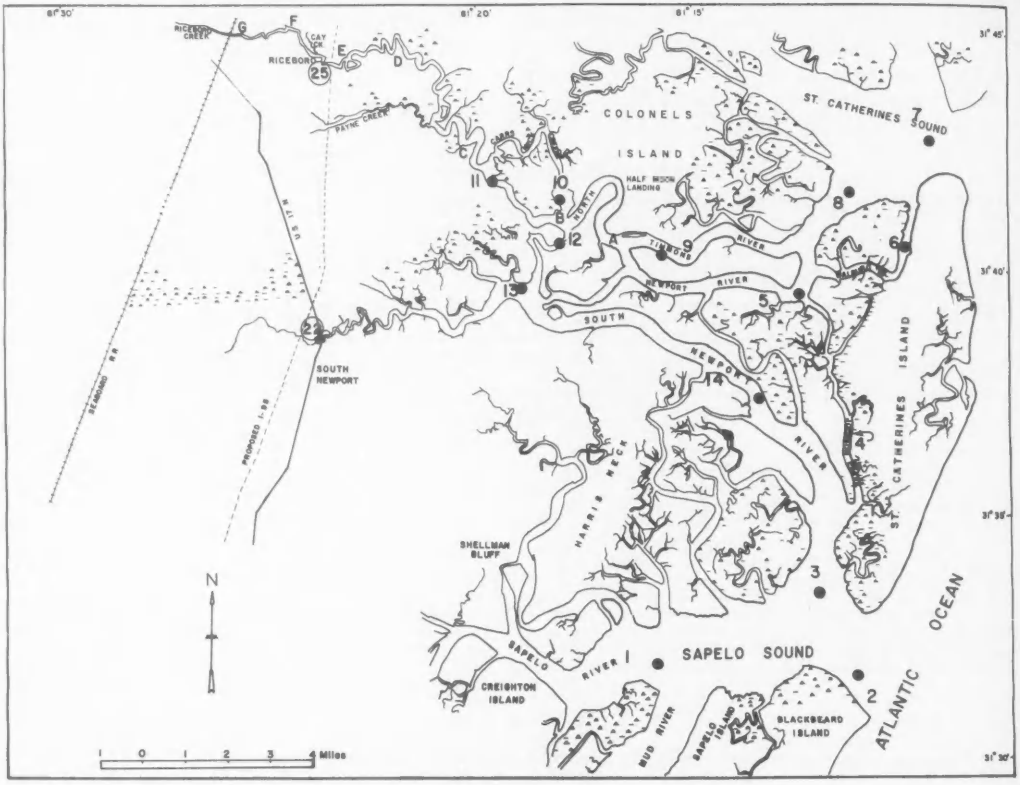

FIGURE 1.—Study area and sampling stations on Georgia Coast except for Sapelo Island and freshwater stations. Numbers 1-14 are trawl stations and associated dots are approximate centers of drags. Letters A-G are stations that were reached with a small boat. Circled numbers are mile points.

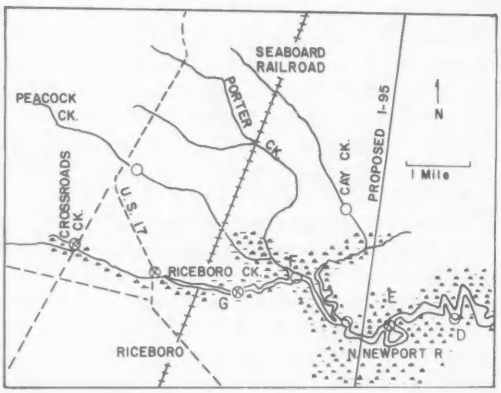

FIGURE 2.—Oligohaline creeks and upper reach of the estuary. Circles are stations sampled for physico-chemical data and circles with an X are fish sampling stations. The Interstate Paper Corp. outfall is at station G. Dashed lines represent highways.

the junction of the road and the beach. Because collecting was generally unproductive in the surf zone at high tide, this station was occupied near low tide. Furthermore, concentrations of fishes in the intertidal sloughs were isolated from the ocean only at low tide.

The continuity of the south end of Sapelo Beach and the lower reach (Doboy Sound) make

FIGURE 3.—View of Sapelo Beach at low tide with Atlantic Ocean and shrimp boat in background and an intertidal slough in center. Fishes become concentrated and trapped in these sloughs at low tide.

it necessary to arbitrarily define the beach habitat to include waters occurring within the wading depth of collectors (about 4 ft). The station is subject to tidal changes—tide ranges from 4.5 to 10.5 ft and has a mean of 6.8 at Sapelo Island (Ragotzkie and Bryson, 1955).

Habitat 2: Lower reach of the estuary. — This habitat includes the sounds and polyhaline river stations. My records for this habitat are based primarily on trawl collections at stations 1-9 and 12-14 (Figure 1). A temperature-salinity diagram (Figure 4) does not indicate any relation between these factors.

Habitat 3: High marsh. — This habitat is the upper section of the littoral zone in the salt marsh. I sampled pools behind high marshes and a tidal ditch in a high marsh but not the high marsh proper. Fishes of this habitat were thoroughly surveyed by Miller and Jorgenson (1969) and are listed in column three of Table 2. Their marsh stations were located near Jekyll Island and near Doboy Sound. The substrate of this habitat is sand and mud that is firm enough to walk on, as opposed to the low marsh which has a soft mud substrate.

Habitat 4: Middle and upper reaches of the estuary (Figures 2 and 5). — The middle reach

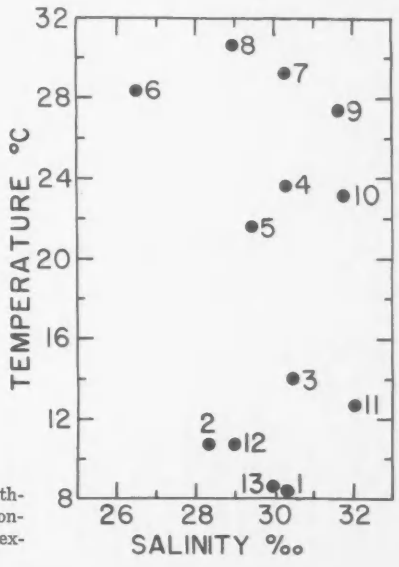

FIGURE 4.—Temperature-salinity diagram for St. Catherines Sound at trawl station 7. Numbers represent consecutive months from January 1968 to January 1969 except 12 is December 1969.

TABLE 2.—Distribution of fishes among the study habitats—1, beach; 2, lower reach; 3, high marsh; 4, middle and upper reaches; 5, oligohaline creek; 6, freshwater creek; 7, tidal canal; 8, low-salinity tidal pool; and 9, high-salinity tidal pool. Names are in phylogenetic order, following Bailey (1970). Parentheses indicate records not taken at regular stations. Boldface indicate record is based on one collection by either the author or Miller and Jorgenson (1969). Asterisk indicates that young of the species are common in the estuary or beach waters. All high marsh records are from Miller and Jorgenson (1969).

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Orectolobidae									
Ginglymostoma cirratum	(X)	(X)							
Carcharhinidae									
**Aprionodon isodon*	(X)	(X)							
Carcharhinus acronotus	(X)	(X)							
**Carcharhinus limbatus*	(X)	X							
**Carcharhinus milberti*	(X)	(X)							
Galeocerdo cuvieri	(X)	(X)							
**Negaprion brevirostris*	X	(X)							
Sphyrnidae									
**Sphyrna lewini*	(X)	(X)							
Sphyrna tiburo		X							
Squalidae									
Squalus acanthias		X							
Rhinobatidae									
Rhinobatis lentiginosus		X							
Rajidae									
Raja eglanteria		X							
Dasyatidae									
**Dasyatis americana*	(X)	X							
**Dasyatis sabina*	X	X		X					
Dasyatis sayi	(X)	X							
**Gymnura micrura*		X		X					
Myliobatidae									
Rhinoptera bonasus	(X)	(X)							
Lepisosteidae									
Lepisosteus osseus		X		X	X	X			
Lepisosteus platyrhincus						X			
Elopidae									
**Elops saurus*	X		X	X			X	X	X
**Megalops atlantica*	(X)	X					X	X	X
Albulidae									
Albula vulpes	(X)								
Anguillidae									
**Anguilla rostrata*			X		X	X		X	X
Ophichthidae									
Myrophis punctatus	(X)		X		X				
Ophichthus gomesi		X							
Clupidae									
Alosa aestivalis		(X)	X	(X)	(X)	(X)			
Alosa mediocris	(X)	X		(X)	(X)	(X)			
**Alosa sapidissima*		X		X	(X)	(X)			
Brevoortia smithi	X		X				X		X
**Brevoortia tyrannus*	X	X	X	X	X		X	X	X
Dorosoma cepedianum	(X)	(X)	X	X	X	(X)			
**Dorosoma petenense*	X		X				X		
Harengula pensacolae	X	X	X						
**Opisthonema oglinum*	(X)	X	X						
Sardinella anchovia	(X)								

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Engraulidae									
Anchoa cubana	(X)								
**Anchoa hepsetus*	X	X	X	X					
Anchoa lyolepis	(X)								
**Anchoa mitchilli*	X	X	X	X	X				X
Esocidae									
Esox americanus					X	X			
Umbridae									
Umbra pygmaea						X			
Synodontidae									
Synodus foetens	(X)	X			X				
Cyprinidae									
Notemigonus crysoleucas					X	X			
Notropis maculatus						X			
Catostomidae									
Erimyzon sucetta						X			
Ictaluridae									
**Ictalurus catus*				X	X	X			
Ictalurus natalis						X			
Noturus gyrinus					X	(X)			
Ariidae									
**Bagre marinus*	(X)	X		X					
**Arius felis*	X	X		X					
Amblyopsidae									
Chologaster cornuta						X			
Aphredoderidae									
Aphredoderus sayanus					X	X			
Batrachoididae									
**Opsanus tau*	X	X		X					
Gobiesocidae									
**Gobiesox strumosus*		X		X					
Antenariidae									
Antennarius radiosus	(X)								
Histrio histrio	(X)								
Gadidae									
**Urophycis floridanus*		X		X					
**Urophycis regius*	(X)	X		X					
Ophidiidae									
Rissola marginata	(X)	X		X					
Belonidae									
Strongylura marina	X	X	X	X					
Cyprinodontidae									
**Cyprinodon variegatus*	X		X				X	X	X
Fundulus chrysotus						X			
**Fundulus confluentus*					X	X		X	
**Fundulus heteroclitus*	X	X	X	X	X		X	X	X
**Fundulus luciae*	(X)		X						
**Fundulus majalis*	X		X				X		X
Fundulus notti						X			

TABLE 2.—Continued.

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Cyprinodontidae—Cont.									
Leptolucania ommata						X			
Lucania goodei						X			
Poeciliidae									
**Gambusia affinis*	X		X		X	X	X	X	X
Heterandria formosa			X		X	X			
**Poecilia latipinna*	(X)		X		X		X	X	X
Atherinidae									
**Membras martinica*	X	X	X						
**Menidia beryllina*	X			X	X	X			
**Menidia menidia*	X	X	X	X					X
Syngnathidae									
Hippocampus erectus		X							
**Syngnathus fuscus*	X	X		X	X				
**Syngnathus louisianae*	X	X	X	X	X				X
Centropomidae									
**Centropomus undecimalis*							X	X	X
Serranidae									
Centropristis philadelphica	(X)	X							
Centropristis striata		X		X					
Centrarchidae									
Acantharchus pomotis						X			
Centrarchus macropterus					X	X			
Elassoma evergladei						X			
Elassoma zonatum						X			
Enneacanthus gloriosus						X			
Enneacanthus obesus						X			
Lepomis auritus					X	X			
Lepomis gulosus					X	X			
Lepomis macrochirus					X	X			
Lepomis marginatus						X			
Lepomis punctatus					X	X			
Micropterus salmoides					X	X			
Percidae									
Etheostoma fusiforme						X			
Pomatomidae									
Pomatomus saltatrix	X	X	X	X					
Echeneidae									
Echeneis naucrates	(X)	(X)							
Carangidae									
Caranx hippos	X	(X)	X	X					X
Caranx latus	(X)								
**Chloroscombrus chrysurus*	X	X	X	X					X
**Oligoplites saurus*	X		X	X					X
Selene vomer	X	X							
**Trachinotus carolinus*	X		X						
**Trachinotus falcatus*	X		X						
Trachinotus goodei	(X)								
Vomer setapinnis	(X)								
Lutjanidae									
Lutjanus griseus	(X)	(X)	X					X	X

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Gerreidae									
**Diapterus olisthostomus*	X		X		X		X	X	X
**Eucinostomus argenteus*	X	X	X	X	X		X	X	X
Eucinostomus melanopterus					X				
Pomadasyidae									
Orthopristis chrysoptera	(X)	X		X					
Sparidae									
**Archosargus probatocephalus*	(X)	(X)	X						
**Lagodon rhomboides*	(X)	X	X				X	X	X
Sciaenidae									
**Bairdiella chrysura*	X	X	X	X	X		X	X	X
**Cynoscion nebulosus*	(X)	X	X	X					X
**Cynoscion nothus*		X							
**Cynoscion regalis*	X	X	X	X			X		X
**Larimus fasciatus*	X	X							
**Leiostomus xanthurus*	X	X	X	X	X		X	X	X
**Menticirrhus americanus*	X	X	X	X					
**Menticirrhus littoralis*	X	X	X						
**Menticirrhus saxatilis*	X	X	X						
**Micropogon undulatus*	X	X	X	X	X		X		X
**Pogonias cromis*	(X)	X	X				X	X	X
**Sciaenops ocellata*	X	(X)	X				X	X	X
**Stellifer lanceolatus*	X	X		X					
Kyphosidae									
Kyphosus incisor	(X)								
Ephippidae									
**Chaetodipterus faber*	X	X	X	X					
Pomacentridae									
Abudefduf saxatilis	(X)								
Mugilidae									
**Mugil cephalus*	X	(X)	X	X	X		X	X	X
**Mugil curema*	X	(X)	X	X			X	X	X
Sphyraenidae									
Sphyraena guachancho	X								
Sphyraena picudilla	(X)								
Uranoscopidae									
**Astroscopus y-graecum*	X	X	X	X					
Blenniidae									
**Chasmodes bosquianus*	(X)	(X)							
Hypleurochilus geminatus	(X)	X							
**Hypsoblennius hentzi*	(X)	X		X					
Eleotridae									
**Dormitator maculatus*								X	
Gobiidae									
Evorthodus lyricus									(X)
**Gobionellus boleosoma*	X		X						X
Gobionellus hastatus		X							X
**Gobionellus shufeldti*	(X)							X	
Gobionellus smaragdus									X
**Gobiosoma bosci*	X	X	X	X	X				
**Gobiosoma ginsburgi*	(X)	(X)							X
Microgobius thalassinus									X

TABLE 2.—Continued.

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Trichiuridae									
Trichiurus lepturus	(X)	X							
Scombridae									
Scomberomorus cavalla	(X)								
Scomberomorus maculatus	X	X							
Stromateidae									
Peprilus alepidotus	X	X		X					
Peprilus triacanthus	(X)	X		X					
Triglidae									
**Prionotus carolinus*	(X)	X							
**Prionotus evolans*	X	X	X	X					
Prionotus salmonicolor		X							
**Prionotus scitulus*	(X)	X		X					
**Prionotus tribulus*	(X)	X		X					
Bothidae									
**Ancylopsetta quadrocellata*		X		X					
Citharichthys spilopterus	(X)	X		X	X				
Bothidae—Cont.									
Etropus crossotus	(X)	X							
Paralichthys albigutta	(X)	X							
**Paralichthys dentatus*		X	X		X				
**Paralichthys lethostigma*		X	X	X	X				
Paralichthys squamilentus		X							
Scophthalmus aquosus		X	X		X				
Soleidae									
**Trinectes maculatus*	(X)	X		X	X	X			
Cynoglossidae									
**Symphurus plagiusa*		X	X	X	X				X
Ballistidae									
Monacanthus hispidus		X	X	X					
Tetraodontidae									
Sphoeroides maculatus		X	X	X					
Diodontidae									
Chilomycterus schoepfi		X	X	X					

includes the North Newport River and lower parts of its tributaries from the lower end of Carrs Neck Creek (trawl station 10) upstream to station C. The upper reach extends from Payne Creek to the mouth of Riceboro Creek (station F). I generally treat these two sections as a unit for convenience.

Because salinity varies so greatly, this section of the estuary only roughly corresponds to the zones recognized by Carriker (1967). He recognized salinity ranges of 5 to 18‰ for the upper reach and 18 to 25‰ for the middle reach.

Habitat 5: Oligohaline creek (Figure 6). — The North Newport River originates at the confluence of Peacock and Riceboro Creeks. Oligohaline sampling stations were located in the oligohaline section of Riceboro Creek (Figure 2). Most fishes were collected in Riceboro Creek at station G and the lower part of Crossroads Creek where it joins Riceboro Creek near the town of Crossroads. Crossroads Creek was recently diverted into Riceboro Creek above the station by the State Highway Department, thus eliminating the station. Salinity and temperature ranges are given in Table 1. A temperature-salinity diagram (Figure 7) indicates that salinity generally increased with rising tide except when fresh water prevailed throughout the tidal cycle. In winter water temperatures were lowest at low tides.

Habitat 6: Freshwater creek. — Seven freshwater or limnetic stations in Coastal Plain creeks, free from the influence of salt water, are called "freshwater stations" in the text. The first six of these stations are in the North Newport River drainage in Liberty County and were sampled on 13 May 1968. The seventh is in the Ogeechee drainage in Chatham County and was occupied on 9 March 1969. Location of these collections are as follows: (1) Upper South Newport River at U.S. Highway 17; (2) Headwaters of Payne Creek on U.S. Highway 17, 2 miles west of Riceboro; (3) Tributary of Riceboro Creek about 2.5 miles north of Crossroads on a county road; (4) Peacock Creek, 2 miles southeast of McIntosh, on dirt road off U.S. Highway 82; (5) Goshen Swamp Creek on U.S. Highway 82, 2 miles south of Flemington; (6) Peacock Creek at Solomon Temple, between

FIGURE 5.—A muddy sand bar exposed at low tide at the mouth of Payne Creek where fishes were seined. *Spartina alterniflora* is visible on the right and the "back marsh" contains *S. alterniflora* and *Juncus roemerianus*. Hammocks and larger islands in this region are bordered by salt marshes and tidal creeks.

FIGURE 6.—Riceboro Creek near high tide at the Seaboard Railroad bridge. A variety of invertebrates are associated with the diverse intertidal flora, roots, and debris found in this oligohaline creek.

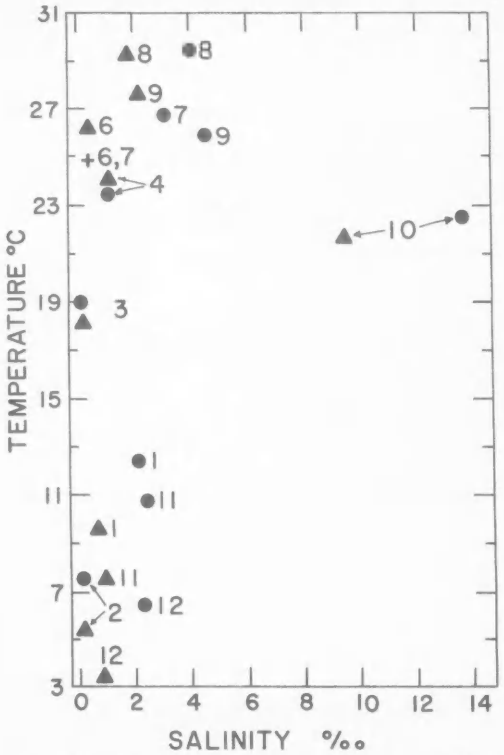

FIGURE 7.—Temperature-salinity diagram for Riceboro Creek at U.S. Highway 17; Numbers 1-4 are months of January through April 1969, and 6-12 are June through December 1968. Circles are high tide readings and triangles are low tide readings. Cross is high tide value for June and low tide value for July.

Midway and McIntosh on dirt road off U.S. Highway 82; (7) Tributary of Ogeechee River at U.S. Highway 17 near the Ogeechee River bridge.

Habitat 7: Tidal canal — This station is a runoff ditch or canal located in the marsh on the west side of Sapelo Island, 3.4 miles north of the Sapelo airport. This ditch is open to a polyhaline river (Mud River) at all tide levels and its mud banks are under several feet of water at high tide. Water depth was 3 to 4 ft at low tide in the deepest section, which was located at the end of a road culvert on the salt marsh side of a road.

Habitat 8: Low-salinity tidal pools — Two small pools located next to the road on the west side of Sapelo Island are treated together in the text. These pools are located 4.1 miles north of the Sapelo airport on the west side of the road. Runoff water flooding through a culvert opening into the lower and larger pools has eroded the bottom to a depth of approximately 5 ft. A higher culvert opening to the upper and smaller pool rarely has runoff water. This pool is 3 to 4 ft deep. At low tide only trickles of water connect the two pools and drain the lower pool through the marsh. Located behind the high marsh, these pools are flooded by Mud River only on high tide.

Habitat 9: High-salinity tidal pools (Figure 8). — These are a series of artificial pools located on the south end of Sapelo Island along a road leading to the Sapelo lighthouse, hence the local name lighthouse ponds. The pools are located behind a high marsh characterized by *Spartina alterniflora* and *Juncus roemerianus*. The pool sampled on the west side of the road is flooded by waters from South End Creek and the Marine Institute's boat basin. Two pools sampled on the east side of the road are connected at high tide and are flooded by waters from Deans Creek. *Palaemonetes pugio* was abundant in seine collection, except during the coldest weeks when the water temperature approached 8°C. At this time the fishes were also scarce or absent, and the relatively sterile and clear water allowed the author to see the bottom of the pools whereas the water was very turbid during other months.

METHODS

I seined shallow estuarine habitats (habitats 1, 5, 7, 8, and 9 and 4 in part) with a 35-ft (10.7-m) seine having ¼-inch (6.35-mm) bar mesh; a 10-ft (3.05-m) version was used in freshwater creeks. For habitat 3 I used the records of Miller and Jorgenson (1969) who collected with 40- and 70-ft (12.2- and 21.4-m) bag seines. Their records for St. Simons Island Beach are included in the list for habitat 1.

Habitat 2 (trawl stations 1-9, 12-14 in Figure 1) and the lower part of habitat 4 (trawl

FIGURE 8.—Tidal "borrow pool" on west side of road to lighthouse on Sapelo Island. Zonation of dominant plants along road bank generally from left to right in picture: wax myrtle (*Myrica cerifera*), groundsel-tree (*Baccharus halimifolia*), marsh elder (*Iva frutescens*), and sea ox-eye (*Borrichia frutescens*). *Juncus roemerianus* and *Spartina alterniflora* are dominant along the pool bank. There is an abundance of crabs (*Uca* spp. and *Sesarma* sp.) in both the harder and softer substrates between the pool and the road.

stations 10 and 11) were sampled on RV *Kit Jones* cruises, each station for 15 min with a 20-ft (6.1-m) otter trawl which had 1¼-inch (32-mm) stretched mesh in the bag. Each of the 14 trawl stations was sampled about 37 times from January 1967 through December 1969 except for stations 6, 8, 12, and 13, which were sampled 33 or 34 times and then discontinued. Five trawl samples were lost for various reasons including snags at station 9 on two occasions.

All Sapelo Island habitats (1, 7, 8, and 9) were sampled during all four seasons and about 20 times from April 1967 through February 1970.

Habitat 4 was sampled primarily with a 20-ft (6.1-m) trawl and a 35-ft (10.7-m) seine. The two trawl stations (10 and 11) are the uppermost of the 14 stations sampled with the RV *Kit Jones* from January 1967 through December 1969. Seining stations were sand bars that were exposed only near low tide. Regular stations were at the lower end of Carrs Neck Creek (mile point 10 = 16.1 km) and the mouth of Payne Creek (mile point 15.4 = 24.8 km). These stations were seined approximately monthly from June 1969 to May 1970. In addition 22 collections were made between the upper end of Carrs Neck Creek and mouth of Riceboro Creek with the seine, a cast net, and a 10-ft (3.05-m) trawl towed by an outboard motor boat.

In habitat 5 most fish collections were seined at low tide at a muddy sand bar (station G) between the Seaboard Railroad tracks and the effluent outfall of the Interstate Paper Corp. Trawling (10-ft trawl) was most fruitful in the winter. Seine and dip-net collections were made at the Crossroads station.

A few additional collections were made with a 100-ft (30.5-m) seine in habitat 1, by angling in habitats 1 and 2 (Dahlberg and Heard, 1969),

and by dip net in habitat 8 and in Riceboro Creek at the Seaboard Railroad.

All specimens were preserved in 10% formaldehyde solution and analyzed in the laboratory except when numbers in trawls were too large to retain more than a sample. Representatives of all species were retained at the Marine Institute.

The phylogenetic order and names recommended by Bailey (1970) are followed herein.

HABITATS OF COASTAL FISHES

ORDER SQUALIFORMES - SHARKS

Ten species of sharks (Table 2) were collected in this study and by Dahlberg and Heard (1969). Nearly all specimens, bonnethead excepted, were caught with fishing poles at the beach and in the sounds. Only three sharks were trawled, one each of the spiny dogfish (*Squalus acanthias*), bonnethead (*Sphyrna tiburo*), and the blacktip shark (*Carcharhinus limbatus*).

Most shark species have distinct seasonal migratory patterns. Carcharhinid sharks apparently migrate into the estuary during the warm months as all six were collected from June to September. The spiny dogfish is a cold-water species that migrates into Georgia estuaries during the coldest months (Dahlberg and Heard, 1969); it was collected only in January and February.

ORDER RAJIFORMES - SKATES AND RAYS

The Atlantic guitarfish (*Rhinobatos lentiginosus*) and clearnose skate (*Raja eglanteria*) are most common in the ocean and were not collected farther up the estuary than the sounds. Although the guitarfish was collected only in May and June, the skate was taken throughout the year.

Three stingrays of the genus *Dasyatis* (Table 2) are common in the sounds and shallow waters along the beaches. The Atlantic stingray (*D. sabina*) was the most abundant of the three species taken by trawling and angling. It was commonly trawled in the middle reach of the estuary at salinities as low as 9.9‰. This species is euryhaline (Gunter, 1956).

The smooth butterfly ray (*Gymnura micrura*) was collected by trawl in the estuary as far up as the middle reaches but not at salinities lower than 24.4‰.

ORDER SEMIONOTIFORMES

Lepisosteidae - gars

Two species of *Lepisosteus* were taken in the study area. The Florida gar (*L. platyrhincus*) occurred only at freshwater station 2. The euryhaline longnose gar (*L. osseus*) was abundant and was often seen or trawled in fresh and brackish waters throughout the year. The longnose gar has been collected in the ocean off Georgia.

ORDER ELOPIFORMES

Elopidae - tarpons

Small ladyfish (*Elops saurus*) were common in enclosed waters of tidal pools and the tidal ditch. Only two specimens were collected in open waters, one at Sapelo Beach and one in the upper reach of North Newport River. The ladyfish was common in both the high- and low-salinity pools at a salinity range of 0.1 to 28.7‰. It entered the pools in May and remained until November when the temperature was 19.9°C.

Small tarpon (*Megalops atlantica*) were common in enclosed waters of tidal pools and the tidal ditch, and large tarpon were often hooked by anglers along Sapelo Beach. Young were collected only from July to October at a temperature range of 20.0° to 31.9°C and were more common in the low-salinity pools than the high-salinity pools; the recorded salinity range was 0.1 to 24.8‰. Rickards (1968) found tarpon at Sapelo Island from July to November at salinities of 0.0 to 22.3‰ and temperatures of 16° to 36°C.

Albulidae - bonefishes

Inclusion of the bonefish (*Albula vulpes*) in Table 2 is based on a record from St. Simons Beach (Miller and Jorgenson, 1969).

ORDER ANGUILLIFORMES

Anguillidae - freshwater eels

The catadromous American eel (*Anguilla rostrata*) was widely distributed and abundant in the freshwater habitat and the high-salinity pools, but absent from trawl stations. All small specimens (54-170 mm) occurred in low salinities (0-1.9‰) in the freshwater and oligohaline creeks, and the low-salinity pools. Large specimens (230-470 mm) occurred primarily in saline waters (13.1-30.3‰) but one was collected in fresh water.

Ophichthidae - snake eels

One speckled worm eel (*Myrophis punctatus*) was collected with a dip net in Riceboro Creek under the Seaboard Railroad bridge. The 243-mm specimen was taken at a salinity of 0‰ and temperature of 24°C. Miller and Jorgenson (1969) also reported it from the beach and high marsh habitats.

Three shrimp eels (*Ophichthus gomesi*) were trawled in the lower reach at stations 4, 7, and 9. They probably burrow and easily escape the trawls. I have also seen specimens of the pale-spotted eel (*O. ocellatus*) from the Georgia coast.

ORDER CLUPEIFORMES

Clupeidae - herrings

Three anadromous species of shad (*Alosa*) are listed (Table 2) for the habitats along their migratory route. I collected the American shad (*A. sapidissima*) and hickory shad (*A. mediocris*) only in saline waters. Both of these species and the blueback herring (*A. aestivalis*) spawn in the nearby Altamaha River (Godwin and Adams, 1969).

Young American shad were occasionally collected from the lower reach to the upper reach from December to April. Since the spawning season of the American shad is from March through May in the Altamaha River (Godwin and Adams, 1969), 60- to 114-mm specimens collected from December to March were approximately 1 year old, and a 29-mm shad collected in April was recently spawned. Both age groups were represented in the upper reach but only individuals of age group I were taken in the middle and lower reaches.

Two species and a hybrid of menhaden (*Brevoortia*) (Dahlberg, 1970) occur within the estuary. The Atlantic menhaden (*B. tyrannus*) occurred in eight habitats. Compact schools of adults occurred in the lower reach of the estuary and along the beaches from spring through fall. Smaller numbers were present in the sounds in the winter. Juveniles (29-42 mm) were often collected from June to September in the upper reach where salinity ranged from 0.5 to 16.8‰ and temperature, from 28.4° to 30.8°C. Juveniles were also collected in the oligohaline Riceboro Creek and this species is known to occur in fresh water (Gunter, 1956). Young menhaden (30-99 mm) also occurred in the tidal pools and tidal ditch in May and June.

The yellowfin menhaden (*B. smithi*) was collected in the high-salinity pools, tidal canal, and along the beach. Its absence from trawl collections supports my theory (Dahlberg, 1970) that *B. smithi* is a bay or shallowwater species. The occurrence of this species apparently is restricted by low temperature as it first appeared in May and was present until water temperature decreased to approximately 20°C in November. Its absence after November may result from a southward migration since it is common along Florida in the winter (Dahlberg, 1970).

The hybrid (*B. smithi* × *B. tyrannus*) was the least common of the menhadens. It was collected with *B. smithi* on 5 May 1969 in the tidal canal which had a salinity of 18.8‰ and a temperature of 29°C. Hybrids were collected also along the beach and in the Marine Institute's boat basin at Sapelo Island.

The gizzard shad (*Dorosoma cepedianum*) and threadfin shad (*D. petenense*) are euryhaline species that are important forage fishes in Georgia reservoirs. The gizzard shad is known from the upper reach and the oligohaline creek from two trawl collections made on 19 November 1969. These large gizzard shad (205-220 mm) were collected at water temperatures of 15.5° and 14.1°C, and others were caught in the Marine Institute's boat basin (lower reach habitat) in the summer of 1969.

The occurrence of the threadfin shad at Sapelo Island may have resulted from recent introduction of this species in the Altamaha and Savannah River drainages by the Georgia Game and Fish Commission. Movement to the north through estuarine waters is also possible. This species was taken in water as saline as 29.8‰ and over a temperature range of 26.0° to 30.6°C.

The scaled sardine (*Harengula pensacolae*) and Atlantic thread herring (*Opisthonema oglinum*) were occasionally collected in the higher salinity waters of the beach, lower reach, and high marsh habitats. The Spanish sardine (*Sardinella anchovia*) was reported from St. Simons Beach by Miller and Jorgenson (1969).

Engraulidae - anchovies

Of four species of anchovies known from Georgia, only the striped anchovy (*Anchoa hepsetus*) and bay anchovy (*A. mitchilli*) were common and widely distributed in the estuary. The bay anchovy was one of the most abundant fish species in trawl and seine collections. It was often collected in fresh waters of the oligohaline creek and upper and middle reaches, but was absent from protected waters with low salinity. The bay anchovy was present throughout the year at a temperature range of 7.9° to 32.0°C. The striped anchovy was found in fewer habitats than the bay anchovy, and it occurred only during warmer seasons, May to November, at a temperature range of 15.7° to 30.8°C.

Two tropical species (*A. cubana* and *A. lyolepis*) were collected at St. Simons Beach (Miller and Jorgenson, 1969) but were not collected at Sapelo Beach.

ORDER SALMONIFORMES

Esocidae - pikes

The pickerel (*Esox americanus*) was collected at five freshwater stations. On 16 December 1969, one specimen was trawled in lower Riceboro Creek where the salinity was 0.3‰ and the temperature, 7.4°C.

Umbridae - mudminnows

The little-known eastern mudminnow (*Umbra pygmaea*) was collected at freshwater station 6, the Ogeechee River tributary. This Coastal Plain species is rare in collections from Georgia waters.

ORDER MYCTOPHIFORMES

Synodontidae - lizardfishes

Only one species (*Synodus foetens*) of the lizardfishes ranges inshore in Georgia estuaries. Six specimens were collected by trawls in 1967 and one by a seine in 1969 in the lower and middle reaches from June to November when the salinity was 16.7 to 32.0‰ and temperature was 16.3° to 31.5°C.

ORDER CYPRINIFORMES

Cyprinidae - minnows and carps

Three species of the freshwater cyprinids were collected. Some large carp (*Cyprinus carpio*) were caught in the lower Atlamaha River during the spring and some apparently moved to Doboy Sound and off Sapelo Beach with the flood waters that reduced salinities to 6.8‰ along Sapelo Beach. Three large carp were found dead on Sapelo Beach in April 1970. Some survived in a low-salinity tidal creek that was temporarily dammed on Sapelo Island until June when they were found dead. The alien carp is not known from the North Newport River headwaters.

The golden shiner (*Notemigonus crysoleucas*) was common in the freshwater habitat, and three juveniles (20-24 mm) were collected in the oligohaline creek on 4 September 1969 when the salinity was 0‰ and temperature was 26.4°C. The golden shiner is a common bait and forage fish in Georgia.

The little-known taillight shiner (*Notropis maculatus*) was taken only at freshwater station 4.

Catostomidae - suckers

The lake chubsucker (*Erimyzon sucetta*) was collected at freshwater stations 1, 4, and 6.

ORDER SILURIFORMES

Ictaluridae - freshwater catfishes

Three species of freshwater catfishes were collected. The yellow bullhead (*Ictalurus natalis*) was common in freshwater stations. A 16-mm tadpole madtom (*Noturus gyrinus*) wandered downstream from its typical freshwater habitat to the Crossroads station where the salinity was 1.9‰. The white catfish (*I. catus*) ranged down the estuary to the middle reach (trawl stations 10 and 11) when the salinity was reduced to 11.7 and 9.2‰ and temperatures were 11.1° and 10.8°C, in January and February. White catfish were seined and trawled (10-ft trawl) on nine occasions in the oligohaline creek at salinities less than 1‰ and at a temperature range of 7.4° to 28.4°C. Large samples including specimens over a length range of 40 to 300 mm, trawled in January and February 1970, suggest that large numbers of white catfish moved into the oligohaline creek when temperatures were 8.6° and 10.0°C. The low temperatures could also reduce their mobility and ability to avoid the trawl.

Ariidae - sea catfishes

The sea catfish (*Arius felis*) and gafftopsail (*Bagre marinus*) were most abundant in the lower reach of the estuary but also occurred in the middle reach and beach habitats. Most of the sea catfish (*Arius*) migrated to the ocean in the late autumn and winter and returned to the estuary and beaches in the spring (Table 3). Males orally incubated the marble-sized eggs in June and July. Young with and without yolk sacs were incubated in August until they were 42 mm long or longer. Young lost the yolk sac when they were 37 to 40 mm long. The gafftopsail also is an oral incubator, but none of the few adults collected contained eggs or young. This species is common in the warm months but scarce in the winter.

ORDER PERCOPSIFORMES

Amblyopsidae - cavefishes

The rare swampfish (*Chologaster cornuta*) was collected at freshwater station 7.

TABLE 3.—Length-frequency distribution of the sea catfish, *Arius felis*, collected with a trawl, 1967. There was no June collection.

Length	Apr.	May	July	Aug.	Sept.	Oct.	Nov.
mm							
25-30				4			
31-35				31			
36-40				104	4		
41-45				123	19		
46-50				90	65		
51-55				45	93	8	
56-60				10	72	26	
61-65				2	55	92	1
66-70	1				11	92	2
71-75	1	3		1	3	51	
76-80	3	3			3	22	
81-85	3	5					
86-90	2	24					
91-100		27	2		1		
101-110		7	20				
111-120		1	53		2		
121-130	1		37	16			
131-140		7	7	16	1		
141-150		7	1	3			
151-160		10	8	2			
161-170		2	13	3			
171-180		10	7	8			
181-190		11	3	6			
191-200		11	9	6	1		
200-210		9	5	3			
211-220		5	6	2			
221-230		3	1	2			
231-240		3	2				
241-250		3					
251-260		2					
261-280		2					

Aphredoderidae - pirate perches

The pirate perch (*Aphredoderus sayanus*) was collected at freshwater stations 3, 4, 5, and 7, and one specimen was taken in fresh water in the oligohaline creek.

ORDER BATRACHOIDIFORMES

Batrachoididae - toadfishes

The oyster toadfish (*Opsanus tau*) was often collected in small numbers in trawls in the lower and middle reaches of the estuary throughout the year. This toadfish is sometimes seen in oyster reefs, and one specimen was found in a fouling community on the underside of a floating dock. The collection of only one specimen in the beach habitat can be attributed to the lack of cover. Salinity ranged from 12.4 to 32.0‰ and temperature, from 28.4° to 30.8°C.

ORDER GOBIESOCIFORMES

Gobiesocidae - clingfishes

The habitats of the small skilletfish (*Gobiesox strumosus*) are similar to those of toadfish. It is usually associated with oyster reefs or bottoms that provide cover, especially shell bottoms. The skilletfish occurred in small numbers in the lower and middle reaches throughout the year.

ORDER LOPHIFORMES

Antennariidae - frogfishes

Two species of frogfishes (Table 2) collected at St. Simons Beach (Miller and Jorgenson, 1969) are stragglers from offshore. The sargassumfish (*Histrio histrio*) is often associated with sargassum weed, which drifts onto Sapelo Beach.

ORDER GADIFORMES

Gadidae - codfishes

The southern hake (*Urophycis floridanus*) and spotted hake (*U. regius*) were common in the trawl collections in the lower and middle reaches from January to May. These southern representatives of a group that inhabit cold water first entered the estuary when the temperature was 8.2° to 10.1°C in January, and they remained until it rose to 24.3° to 24.6°C. Salinity and temperature ranges were 12.4 to 30.6‰ and 9.0° to 24.6°C for *U. floridanus*, and 14.5 to 31.1‰ and 8.2° to 24.3°C for *U. regius*. Miller and Jorgenson (1969) also reported four *U. regius* from St. Simons Beach.

Ophidiidae - cusk-eels

This family is represented by one species, the striped cusk-eel (*Rissola marginata*), in Georgia estuaries. Small numbers of this burrowing species were collected throughout the year by trawling in the lower and middle reaches at salinities of 11.6 to 32.6‰ and temperatures of 8.0° to 30.0°C.

ORDER ATHERINIFORMES

Belonidae - needlefishes

Several needlefishes range to the Georgia coast, but only the Atlantic needlefish (*Strongylura marina*) is common in Georgia estuaries. It is occasionally seen around docks in the lower and middle reaches and specimens were seined at the beach, high marsh, and middle reach habitats. Specimens (52-315 mm) were collected from May to October at 22.9° to 30.9°C.

Cyprinodonidae - killifishes

These small fishes are found almost entirely in shallowwater habitats. The euryhaline sheepshead minnow (*Cyprinodon variegatus*) was present throughout the year at salinity and temperature ranges of 0.8 to 34.0‰ and 7.9° to 31.9°C in the tidal pools, beach, high marsh, and tidal canal habitats.

The golden topminnow (*Fundulus chrysotus*) was collected at freshwater stations 3 and 5.

The marsh killifish (*F. confluentus*) occurred at freshwater station 1 and at Crossroads but was common only at an artesian well and in the low-salinity tidal pool where it occurred throughout the year. Recorded salinity and temperature ranges were 0 to 24.4‰ and 7.8° to 29.3°C.

The mummichog (*F. heteroclitus*) occurred at all the habitats except the freshwater habitat. Although it is a shallowwater species, two collections were made at trawl stations (10 and 12) that were close to the marsh. The mummichog was common at most seine stations but was rare along the beach. Recorded salinity and temperature ranges were 0 to 34‰ and 7.8° to 32.2°C.

The southernmost record of the spotfin killifish (*F. luciae*) was reported by Miller and Jorgenson (1969).

The striped killifish (*F. majalis*) was present at the Sapelo Beach throughout the year, but was scarce during the coldest months. It was also common in the high marsh and high-salinity tidal pools, and uncommon in the tidal ditch. The striped killifish was not taken at sand bars in the middle reach although it was col-

lected at low salinities. Salinity and temperature ranges were 6.8 to 34.0‰ and 7.0° to 32.2°C.

The last three cyprinodonts listed on Table 2 are freshwater species characteristic of the Coastal Plain. The bluefin killifish (*Lucania goodei*) is also common in fresh water on Sapelo Island.

Poecilidae - livebearers

The euryhaline mosquitofish (*Gambusia affinis*) occurred at seven habitats and was abundant at the freshwater, oligohaline creek, and low-salinity tidal pool stations. It was collected on the beach only when the salinity was 6.8‰, but it was not uncommon at higher salinities. Salinity and temperature ranges were 0 to 34‰ and 7.3° to 30.7°C.

The least killifish (*Heterandria formosa*) is a freshwater species that occasionally wanders into estuarine waters. The highest salinity record was 4.0‰.

The sailfin molly (*Poecilia latipinna*) was common in the shallow protected waters of the tidal pools, tidal ditch, and an artesian well on Sapelo Island. It occasionally occurred in the high marsh, beach, and oligohaline creek habitats. Temperature and salinity ranges were 7.3° to 32.2°C and 0 to 34‰.

Atherinidae - silversides

The rough silverside (*Membras martinica*) was common at the beach and high marsh habitats. It was attracted to artificial lights at night and collected in large numbers with a dip net in the lower reach. Because of their pelagic nature and small size, only one was collected in a trawl.

The Atlantic silverside (*Menidia menidia*) was found in the four high salinity habitats and in the middle and upper reaches of the estuary. This silverside was common only at high salinities, but it occurred at a sand bar in the middle reach when the salinity was 0.9‰ on 4 September 1969. Although collected at a temperature range of 7.0° to 31.5°C, this silverside left the sand bars of the middle and upper reaches at temperatures below 12°C.

The tidewater silverside (*Menidia beryllina*) was common in the freshwater and oligohaline creek habitats at salinities of 0 to 7.9‰. It ranged to the middle reach when the salinity was 0.1‰. One was collected at Sapelo Beach when the salinity was 6.8 to 7.7‰; this was the only occasion the two species of *Menidia* were collected together although their habitats and salinity tolerances overlap.

ORDER GASTEROSTEIFORMES

Syngnathidae - pipefishes and seahorses

One lined seahorse (*Hippocampus erectus*) was collected by trawl in Johnson Creek (station 4) in May 1969 at a salinity of 27.1‰ and a temperature of 22.3°C. The northern pipefish (*Syngnathus fuscus*) was taken sporadically by trawl and seine throughout the year. It occurred in four habitats at a salinity range of 0 to 31.3‰.

The chain pipefish (*Syngnathus louisianae*) was uncommon in all six habitats where it was found. It was taken by trawl and seine throughout the year, but was less common than the northern pipefish. The chain pipefish was collected only 12 times and at a salinity range of 0.7 to 31.6‰.

ORDER PERCIFORMES

Centropomidae - snooks

The snook (*Centropomus undecimalis*) was represented by young (23-81 mm) collected in protected waters of the tidal pools and tidal ditch. These were collected from June to November at salinity and temperature ranges of 0 to 22.1‰ and 23.0° to 28.6°C. Linton and Rickards (1965) collected 64 juveniles (24.1-74.9 mm long) at Sapelo Island in 1963 and 1964. Their low temperature record of 18°C occurred in November.

Serranidae - sea basses

Of the diverse serranids found on the Georgia coast, only two species range inshore to the estuary. Young of the black sea bass (*Centropristis striata*) and rock sea bass (*C. philadelphica*)

were collected throughout the year in the lower reach, mostly over shell bottoms at trawl stations 3 to 6.

Centrarchidae - sunfishes

Twelve centrarchids (Table 2) were common in the creeks of the Coastal Plain. Six species (*Centrarchus macropterus, Lepomis auritus, L. gulosus, L. macrochirus, L. punctatus,* and *Micropterus salmoides*) were also collected in the oligohaline creek. Although sunfishes have marked tolerance for salinity (Bailey, Winn, and Smith, 1954), none of these were found at a salinity above 0.5‰.

Percidae - perches

The swamp darter (*Etheostoma fusiforme barratti*) was collected only at freshwater stations 3, 4, and 5.

Pomatomidae - bluefishes

The bluefish (*Pomatomus saltatrix*) is often caught by anglers in the beach and lower reach habitats but was rarely taken in this study. Only four young (115-196 mm) were collected, one in each season of the year.

Echeneidae - remoras

A sharksucker (*Echeneis naucrates*) is recorded for the lower reach and beach habitats since one was attached to a lemon shark that was caught from the beach in Doboy Sound (Dahlberg and Heard, 1969).

Carangidae - jacks and pompanos

Nine species of carangids occurred primarily in the beach and lower reach habitats. The horse-eye jack (*Caranx latus*) is represented by four specimens from St. Simons Beach (Miller and Jorgenson, 1969). The crevalle jack (*C. hippos*) was occasionally caught by anglers in the lower reach of the estuary and a few juveniles were seined as far up the estuary as the upper reach when the salinity was 10.8‰. Five small specimens (24-77 mm) were collected in the summer and autumn.

The Atlantic bumper (*Chloroscombrus chrysurus*) and leatherjacket (*Oligoplites saurus*) were mostly caught at the high-salinity stations. The lowest salinity recorded for the leatherjacket was 16.8‰. Both occupied shallow waters and the bumper was also caught in trawls.

The lookdown (*Selene vomer*) and Atlantic moonfish (*Vomer setapinnis*) were found in the beach habitat generally from May to November. Lookdowns were occasionally trawled in the sounds.

Young of the commercially important Florida pompano (*Trachinotus carolinus*) and young permit (*T. falcatus*) were common in the beach habitat and occasionally wandered to the high marsh. Young pompano were present from spring to autumn. The palometa (*T. goodei*) was present in summer and autumn at St. Simons Beach (Miller and Jorgenson, 1969), and the permit followed the same pattern at Sapelo Beach.

Lutjanidae - snappers

The gray snapper (*Lutjanus griseus*) spawns offshore, and the young have occasionally been collected in the beach, high marsh, and tidal pools habitats. This primarily tropical species was collected from August to November. The lowest salinity recorded for this species was 13.1‰.

Gerreidae - mojarras

Three species of mojarras, Irish pompano (*Diapterus olisthostomus*), spotfin mojarra (*Eucinostomus argenteus*), and flagfin mojarra (*E. melanopterus*), were collected. The flagfin mojarra was represented in one collection that contained all three species. This unusual collection was at a sand bar in the oligohaline creek on 22 October 1969 when the salinity was 0.7‰ and the temperature was 24°C. The Irish pompano was represented by juveniles collected at six shallowwater habitats. They occurred from July to November at salinities and temperatures of 0.7 to 31.3‰ and 19.4° to 31.8°C.

The spotfin mojarra was collected in seven habitats by seining and was the only mojarra collected (twice) by trawling. This species was

taken from July to November at salinities and temperatures of 0.7 to 31.3‰ and 12.7° to 31.1°C. Dr. C. L. Hubbs identified this species in two collections from Sapelo Beach and Riceboro Creek, and I believe that neither of the closely related species, *E. gula* or *E. jonesii*, occurred in my collections.

Pomadasyidae - grunts

The primarily tropical grunts are represented by the pigfish (*Orthopristis chrysoptera*) in Georgia estuaries. The pigfish was trawled in the lower and middle reaches from June to December and was also collected at the beach. A minimum salinity of 15.4‰ was recorded.

Sparidae - porgies

The sheepshead (*Archosargus probatocephalus*) provides an important sport fishery around docks in the lower reaches and also occurred in the high marsh and beach habitats. The small pinfin (*Lagodon rhomboides*) was rare but widespread (six habitats). Small pinfish (20-87 mm) were present from May to September, and most were collected in the intertidal pools.

Sciaenidae - drums

This is the most important family of fishes in Georgia estuaries to sport fishermen. Sciaenids are the most numerous fishes in terms of numbers available to trawls (Anderson, 1968), and probably most abundant in terms of biomass in trawl collections.

Silver perch (*Bairdiella chrysura*) occupied a variety (8) of habitats. Adults were common only in trawl collections in the lower and middle reaches. The silver perch spawned primarily in April and May (Table 4). The smallest specimens were collected in the lower reach and high-salinity pools in May and June. Two age groups (Table 4) were distinct from May to July. Young grew rapidly from May to October in a wide variety of habitats. They apparently use the whole estuary and also the beach waters as a "nursery ground." Salinity and temperature ranges for this species were 1.3 to 34.1‰ and 7.5° to 32°C.

The spotted seatrout (*Cynoscion nebulosus*) are among the most important estuarine fishes to Georgia anglers. They were occasionally trawled in small numbers in the lower and middle

TABLE 4.—Length-frequency distribution of the silver perch, *Bairdiella chrysura*, collected by trawling and seining, 1967-68.

Length	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
mm												
16-20			3									
21-25			13	6								
26-30			92	6								
31-35			20	14	10							
36-40				8	46							
41-45				1	85	2						
46-50				1	85	8						
51-55				3	66	9	2					
56-60					43	10		1				
61-65					34	15	4	5				
66-70					8	9	7	15		1		
71-75					4	6	7	35	1	2		
76-80						4	13	48	3	2		2
81-85	1		2			4	14	64	5	4	3	5
86-90			1	2		1	14	65	6	5	3	4
91-95	3	7	2	1			6	60	6	4	10	4
96-100	2	1	9	2	1		3	52	4	13	9	1
101-105	1	8	20	5				36	2	8	5	
106-110	4		6	3	1			14			1	1
111-115	2		7		1			4			2	
116-120	1		1		2			1		1		
121-125											1	
126-130											1	
131-135					1							
136-140					1							

TABLE 5.—Length-frequency distribution of weakfish, *Cynoscion regalis*, collected by trawling, 1967-68. None were collected in March.

Length	Jan.	Feb.	Apr.	May	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
mm											
11-20				4	2		2				
21-30				7	42	25	18				
31-40				27	93	66	18	6			
41-50				12	150	55	7	24			
51-60				1	122	24	5	30			
61-70	1				151	17	5	50	1	1	
71-80	1				157	16	9	61	3		
81-90	1			1	141	21	4	66	18	1	
91-100	1				122	28	1	36	24	4	2
101-110	5	1	2	1	95	29		22	18	7	
111-120	1			4	50	41	5	14	5	1	
121-130	1	1	2	11	18	35		9	2	3	1
131-140		1		7	13	25		8	1		
141-150			2	16	6	10		3		1	
151-160				9		4		1			
161-170				3		1					
171-180				1	4	1					
181-190					1						
191-200					1	1					
201-210								1			
211-220								1			
221-230											
231-240		1									

reaches throughout the year. They were rarely seined in shallowwater habitats although many are caught with fishing poles along the beaches and salt marshes. Spotted seatrout are known to spawn in and spend their whole life in the estuary (Tabb, 1966). Juveniles were found as far up the estuary as the upper reach at a salinity of 0.5‰.

During 1967-69, silver seatrout (*Cynoscion nothus*) entered the lower reach of the estuary in May and stayed until July or August.

Weakfish (*Cynoscion regalis*) apparently spawned from April to August (Table 5). With the exception of May samples, age groups are difficult to recognize because of the protracted spawning season. Young weakfish were collected in six habitats. Adults and young were abundant only in trawl collections in the lower and middle reaches. Although most abundant in high-salinity waters, young weakfish occurred at salinities as low as 6.6‰ in the upper reach. Weakfish were conspicuously scarce in the cold months, December to April.

The banded drum (*Larimus fasciatus*) was occasionally collected in the lower reach throughout the year and was collected three times along the beach. It was restricted to high salinities, 22.0 to 34.1‰.

Length frequencies of the spot (*Leiostomus xanthurus*) were based on trawl and seine collections (Table 6). Adults were common in deeper waters and juveniles dispersed to eight shallowwater and deepwater habitats. Young spot (11-85 mm) were among the most numerous fishes of the oligohaline creek where they were collected seven times from April to July at a salinity range of 0.2 to 3.1‰. Young were also common in the tidal pools and tidal ditch. Seine collections indicated that the spot spawned primarily from January to April. Two age groups were distinct from February to May.

The three species of kingfishes (*Menticirrhus*) have marked similarities and differences in their ecologies. All three occurred in the beach and lower reach habitats and were rare in the high marsh. Young southern kingfish (*M. americanus*) were also taken in the middle and upper reaches. It is the only kingfish that was found in low salinities. Four juveniles (19-36 mm) were collected in the upper reach in July and August at salinities of 1.5 to 7.9‰, much lower than the low-salinity limits observed by Gunter (1961).

Seining along Sapelo Beach took young southern kingfish that had been spawned primarily from April to August (Table 7). Young and

TABLE 6.—Length-frequency distribution of the spot, *Leiostomus xanthurus*, collected by seine, 1967-69 (in parentheses) and by trawl in 1967. None were collected in September.

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Oct.	Nov.	Dec.
mm											
11-15		(2)	(3)		(3)						
16-20		(10)	(14)		(2)						
21-25		(6)	(30)	(4)	(1)						
26-30			(12)	(3)	(1)						
31-35				(2)	(6)	(4)					
36-40			(1)	(4)	1 (10)						
41-45				(2)	3 (11)	(2)	(7)				
46-50				(1)	2 (10)		(5)				
51-55				(1)	3 (9)	(3)	2 (9)	(2)			
56-60				(5)	2 (9)	(3)	5 (13)				
61-65				(4)	(5)		6 (6)	(1)			
66-70	4	2			(3)	(3)	7 (3)	1			
71-75	11	10			(1)	(1)	4 (3)				
76-80	12	14			2 (1)	2 (3)	5		3		
81-85	17	12	4		(2)		2 (1)				
86-90	18	14	3				2	1	2 (1)		
91-95	14	18	1	2	2			2			
96-100	19	16	3		4		2	2			1
101-105	23	18	9	2	4		1	2			1
106-110	14	7	7	4	7		1	2			
111-115	21	8	7	2	8			2			
116-120	13	8	11		12		1				
121-125	9	8	7	3	9		1				
126-130	10	5	9	2	10		2	1			
131-135	5	5	10	5	9		2			2	1
136-140	1	2	5	2	9		2				1
141-145	2		4	3	9		5	1		1	1
146-150	2	1		1	4		6			2	3
151-155							7			1	
156-160					1					1	2
161-165					1		2			1	1
166-170							1				

adults also occupied the lower and middle reaches. Although generally common, adults were rare in March and April apparently because they migrate to the ocean where they spawn in offshore waters (Bearden, 1963).

Gulf kingfish (*M. littoralis*) spawned primarily from April to September, judging from 18- to 22-m specimens that were taken along the beach from May to October. The Gulf kingfish was common only along the beach from May to November in my collections.

The northern kingfish (*M. saxatilis*) was the least common of the kingfishes. Young (17-50 mm) occurred along the beach in April and May, and five larger specimens (58-140 mm) were trawled in the lower reach from May to August.

The Atlantic croaker (*Micropogon undalatus*) somewhat resembles the spot (*Leiostomus xanthurus*) in population size and distribution in the estuary. Table 8 indicates that croakers spawned primarily from September to April. Bearden (1964) found that in South Carolina croakers spawned almost entirely in the ocean, and larvae were found from October through May. Young croakers (16-80 mm) were collected in seven habitats, including six shallow-water habitats, at salinities down to 2.7‰. Unlike spots, young croakers were not abundant in shallow water and they did not occur in fresh water. Adult croakers were common in trawl catches in the lower and middle reaches, especially May through August when they were not spawning. The population decline in autumn

TABLE 7.—Length-frequency distribution of the southern kingfish, *Menticirrhus americanus*, collected at Sapelo Beach by seine, 1967-68 (parentheses) and by trawls, 1967.

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
mm												
11-15					1 (4)				(2)			
16-20					1 (33)	(1)	2 (2)	(1)	1 (15)			
21-25					1 (48)	(13)	2 (1)	1 (1)	4 (23)			
26-30					(14)	(24)	19 (14)	21 (2)	11 (7)			
31-35					(2)	(45)	38 (28)	49 (2)	12 (3)	(1)		
36-40						(19)	48 (33)	41	11	6 (2)	1	
41-45					1	(2)	30 (11)	30	5	18	1	
46-50							39 (3)	26	9 (1)	27		
51-55					(1)		15 (1)	28	6	21	2	1
56-60					(2)		15 (2)	29	9	17	3	1
61-65	1				(1)		14	20	8	14	5	1
66-70		2			(1)		15 (3)	21	7	11	3	4
71-75	1	2					16 (2)	12	4	10	8	7
76-80	4	3					19	12	4	7	7	13
81-85	2	6	1				18	16	10	9	6	5
86-90	3	12		1			13	4	4	14	7	4
91-95	4	7					11	9	2	10	6	3
96-100	4	13					7	10	2	5	6	5
101-105	4	6					11	6	2	11	5	2
106-110	1	8	1				1	6	1	6		4
111-115	1	5			2			2	2	10	4	4
116-120	1	6	1		2			1	1	4	5	2
121-125	1	2					1		1	6		1
126-130	1	5			2			1	2	4	2	2
131-135	2				3			2				4
136-140	2	1		1	3		1					1
141-150	3	1	1		4		1	1		3	2	2
151-160	2	1	1		2		2	1		5	2	
161-170	1						2				1	1
171-180	2						2	1				
181-190		1					1	1	1			2
191-200		1			2		3					
201-210	1						1					1
211-220									1			1
221-230										2		1
241-250		1										1

was the result of seaward migration for spawning. Bearden (1964) found ripe croakers 3 to 30 miles offshore. Correlation of movements with spawning is complicated by the protracted (8 months) spawning period.

Large black drums (*Pogonias cromis*) are occasionally caught by fishermen in the lower reach. I collected only a few black drums, all small (19-130 mm), mostly in the high-salinity pools.

The red drum (*Sciaenops ocellata*) is one of the most popular estuarine sport fishes because of its large size and abundance in the beach and lower reach habitats. The red drum was taken in only six seine collections and no trawl collections. The smallest (36 and 37 mm) specimens occurred in November.

The star drum (*Stellifer lanceolatus*) was the most abundant species in the lower reach habitat in 1967 (Dahlberg and Odum, 1970) and also in estuaries near Brunswick in 1933-35 (Anderson, 1968). It is a small species and may account for less biomass than the spot or croaker. Young of the year, apparently spawned from May or June to September (Dahlberg and Odum, 1970), accounted for most of the numbers.

TABLE 8.—Length-frequency distribution of the Atlantic croaker, *Micropogon undulatus*, 1967 and January and February 1968. Most were collected with a trawl. Seine and cast net collections are indicated by parentheses.

Length	1967											1968	
	Jan.	Feb.	Mar.	Apr.	May	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
mm													
16-20											(5)		(1)
21-25					1					(1)	(9)		
26-30					3				1		(6)		
31-35					1				2		(6)		
36-40					2				2	2	(1)		
41-45					3				1	2	2		
46-50		1			10				1		4		1
51-55		2			17	1	1	1		1	1	1	
56-60	1		1		7	1	1	1					2
61-65		2		2	8	5			5			1	1
66-70				1	20	7			11				1
71-75		1		4	17	6			2				
76-80	2	2	1	1	23	13			5	1			
81-85	1			2	25	12	2		8	1	1		1
86-90			1	1	8	18			3	2	2	1	3
91-95			3		7	43	3		5	1	3	3	1
96-100				1	7	47	7		1			2	1
101-105					4	70	6				1	1	
106-110						81	10						4
111-115		1				74	13			1		1	5
116-120		2	1			50	9				2	1	4
121-125	1	1		1		41	10			1		1	1
126-130	1	2				16	5					2	1
131-135		2			1	4	4		1		1		2
136-140						3	3					1	
141-145						3		1					
146-150							1						
151-170								1	1				

Most star drum left the estuary during the cold months.

Kyphosidae and Pomacentridae

These two families were represented only by stragglers from offshore (Table 2). They were collected at St. Simons Beach (Miller and Jorgenson, 1969).

Ephippidae - spadefishes

Small Atlantic spadefishes (*Chaetodipterus faber*) were common in trawls in the lower and middle reaches from June to October at a temperature range of 20.1° to 32.0°C. They were uncommon in shallowwater habitats and were not collected at salinities below 9.9‰.

Mugilidae - mullets

Striped mullet (*Mugil cephalus*) and white mullet (*M. curema*) were widespread and abundant in the estuary. Both species generally occupied shallow water near the surface. The striped mullet was collected in eight shallow-water habitats, and it often enters inland rivers. The white mullet occupied the same estuarine habitats with the exception of the oligohaline creek. This difference may be attributed to salinity preferences since the white mullet was taken at salinities down to 5.0‰ and the striped mullet was often collected at salinities below 0.5‰.

The striped mullet was common or abundant in all the habitats in which it occupied. The white mullet was common in the beach and high-salinity pool habitats. The striped mullet apparently has a greater temperature tolerance since it was collected throughout the year at a temperature range of 7.0° to 31.7°C. The white mullet was absent from collections from January through March and occurred at a temperature range of 15.0° to 32.2°C.

Length frequencies indicated that the striped mullet spawned from September through April and the white mullet from March through September, with some overlap in March, April, and September.

Sphyraenidae - barracudas

Young of two species of barracudas occurred in the beach habitat. One guaguanche (*Sphyraena guachancho*) was collected at Sapelo Beach in October 1967. Three southern sennets (*S. picudilla*) were collected at St. Simons Island Beach in May (Miller and Jorgenson, 1969).

Uranoscopidae - stargazers

The southern stargazer (*Astroscopus y-graecum*) was occasionally trawled in the lower and middle reaches. Young were seined along the beach and in the upper and middle reaches at salinities as low as 12.5‰.

Blennidae - combtooth blennies

Three species of blennies (Table 2) are commonly associated with oyster reefs or patches of oyster shells in the lower reaches of the estuary. The feather blenny (*Hypsoblennius hentzi*) was occasionally trawled in the lower and middle reaches and one crested blenny (*Hypleurochilus geminatus*) was trawled in the lower reach. All three species occasionally occurred along the beach (Miller and Jorgenson, 1969) generally in association with shell or debris.

My data suggest that the feather blenny occurred primarily in deep water in the cold months and that they migrated to the oyster reefs in the warm months where they rear their eggs inside of gaping oyster shells. Three male striped blennies (*Chasmodes bosquianus*), 58 to 64 mm, were rearing embryos inside of gaping oyster shells on 24 April 1970 and 19 May 1970 when water temperature was 27° to 27.5°C.

Eleotridae - sleepers

The fat sleeper (*Dormitator maculatus*) was collected only in the low-salinity tidal pools from May through November in 1967.

Gobiidae - gobies

The lyre goby (*Evorthodus lyricus*) was collected once in the high-salinity pools previous to my collections. All four species of *Gobionellus* were rarely encountered. The darter goby (*G. boleosoma*) was collected three times in the high-salinity tidal pools and was rarely found in the beach or high marsh habitats. Only five specimens of the sharptail goby (*G. hastatus*) were collected—three in trawls, one in the Marine Institute's boat basin, and one in the high-salinity pools. This goby was found only in September 1967 and November 1969.

The freshwater goby (*G. shufeldti*) occurred in the low-salinity tidal pools from May 1967 to February 1968. This goby was also reported in the high-salinity waters of St. Simons Beach and in fresh water of Altamaha River (Miller and Jorgenson, 1969).

The emerald goby (*G. smaragdus*) and green goby (*Microgobius thalassinus*) are two little-known species that were collected only in the high-salinity tidal pools. The former occurred there only in September and November and the latter only in May and November.

Two species of scaleless gobies (*Gobiosoma*) were most abundant in oyster reefs and patches of oyster shells where they laid their eggs inside gaping oyster shells during the warm months. The naked goby (*G. bosci*) occurred in six habitats in addition to oyster reefs and was the most abundant goby in the estuary. It was collected by hand in gaping oyster shells and by seining, and three were trawled. The salinity range was from fresh water to 30.8‰. Only juveniles (18-22 mm) were found at salinities of less than 2‰.

The seaboard goby (*Gobiosoma ginsburgi*) was not collected at regular stations except for specimens from the lower reach that were taken from the stomachs of hakes (*Urophycis*). Males were found rearing embryos inside of gaping oyster shells. On 4 March 1969, a large number of seaboard gobies and a few naked gobies were found in burrows in an eroding clay bank at Sapelo Island Beach.

Trichiuridae - cutlassfishes

The Atlantic cutlassfish (*Trichiurus lepturus*) was occasionally trawled throughout the year in the lower reach but was rare along the beach.

Scombridae - mackerels and tunas

King and spanish mackerels are often caught offshore by sport fishermen during the warm months. Young Spanish mackerel (*Scomberomorus maculatus*) occasionally ranged into the high marsh, beach, and lower reach habitats, but they were rarely collected by seine or trawl because of their speed. One king mackerel (*S. cavalla*) was also collected along the beach (Miller and Jorgenson, 1969).

Stromateidae - butterfishes

The butterfish (*Peprilus triacanthus*) and harvestfish (*Peprilus alepidotus*) are primarily marine fishes that occasionally occur in trawl catches in the middle and lower reaches and in beach seine hauls. They have a wide temperature tolerance as they were collected throughout the year. Butterfish did not occur at salinities below 19.5‰ and harvestfish below 22.8‰.

Triglidae - searobins

Four species of searobins (*Prionotus carolinus, P. evolans, P. scitulus,* and *P. tribulus*) were present in trawl collections in the lower reach throughout the year, and all but *P. carolinus* were trawled in the middle reach. Three of these, excluding *P. evolans,* were occasionally taken in the beach habitat (Miller and Jorgenson, 1969). A salinity of 15.3‰ for *P. evolans* was the lowest I found occupied by searobins. One *P. salmonicolor* was collected in Sapelo Sound.

ORDER PLEURONECTIFORMES

Bothidae - lefteye flounders

The lefteye flounders were represented by eight species that were found only in habitats 1 to 5 (Table 2). Species of *Paralichthys* reach a large size and two of them are important sport and commercial fishes whereas the four other bothids are small. The ocellated flounder (*Ancylopsetta quadrocellata*) and windowpane (*Scophthalmus aquosus*) migrated into the lower and middle reaches during the winter and spring, December or January to May. Water temperature ranges were 8.0° to 26.0°C for the ocellated flounder and 8.8° to 25.7° for the windowpane. These species were seasonally replaced by the bay whiff (*Citharichthys spilopterus*), which was occasionally trawled in the lower and middle reaches from May to October at a temperature range of 26.0° to 31.5°C. Stragglers also occurred in the beach and oligohaline creek habitats.

The fringed flounder (*Etropus crossotus*) was common in trawls in the lower reach throughout the year. There are records from the beach habitat, and a 16-mm specimen was seined in the upper reach when the salinity was 0.5‰.

Two species of *Paralichthys* occur primarily offshore and rarely move inshore. The gulf flounder (*P. albigutta*) was trawled only three times. The broad flounder (*P. squamilentus*) was represented by only one juvenile from the beach habitat.

The summer flounder (*P. dentatus*) and southern flounder (*P. lethostigma*) enter the commercial and sport fisheries of the coast. The summer flounder was most abundant in the lower reach and was rarely trawled in the middle reach. The southern flounder was much more abundant at the middle reach stations than in the lower reach. Its tolerance or preference for lower salinities was also demonstrated by its distribution up the estuary to Riceboro Creek where it was often collected in fresh water.

Soleidae - soles

The hogchoker (*Trinectes maculatus*) is a marine or brackish-water fish that often spends considerable time and travels considerable distances in fresh water. It was common from the lower reach to the freshwater habitat. The hogchoker was present throughout the year in Riceboro Creek where the water was usually fresh.

Cynoglossidae - tonguefishes

The blackcheek tonguefish (*Symphurus plagiusa*) was rarely collected outside of the lower and middle reaches where it was one of the most

abundant species. A low-salinity record of 0.7‰ was obtained from Riceboro Creek.

ORDER TETRAODONTIFORMES

Three marine species (in three families) in this order were represented mostly by small numbers of juveniles. Nearly all specimens were collected in the lower reach and beach habitats. One planehead filefish (*Monacanthus hispidus*) was recorded for a low salinity of 11.8‰. The planehead filefish was in the estuary from April to September at 21.8° to 31.3°C. The northern puffer (*Sphoeroides maculatus*) and striped burrfish (*Chilomycterus schoepfi*) were in the estuary from April to November or December when the temperature was reduced to approximately 11° to 16°C.

LIFE CYCLES OF ESTUARINE SPECIES

Many fishes found in estuaries follow the marine-estuarine life cycle pattern described by Gunter (1967). They spawn in the ocean and the young enter the estuarine and beach waters where the salinity is reduced. The estuary apparently provides them with a nursery ground that is rich in food and a refuge from certain predators, diseases, and parasites that do not thrive in the rigors of highly variable salinities and temperatures. Young of coastal species often have greater tolerance to reduced salinities than adults (Gunter, 1961). Young Atlantic menhaden even require low salinities for development (June and Chamberlin, 1959). Gunter (1967) noted: "The preponderant macroorganisms, both in numbers of species and individuals, are mostly motile species which undergo the general type of life history described above. In southern waters these are the mullet (*Mugil*), menhaden, croakers (sciaenids), shrimp and crabs. Vast numbers of these animals may be found in estuaries at one time or another and in general the very smallest sizes are found in the lower salinities." Some species that spawn in high-salinity waters but were represented predominantly by young in two low-salinity estuarine habitats (oligohaline creek and low-salinity tidal pools) included the spot, striped mullet, hogchoker, southern flounder, ladyfish, tarpon, and snook. The Atlantic menhaden, silver perch, and Atlantic croaker were euryhaline and represented in the upper reach primarily by young.

Since estuaries are being destroyed by pollution, dredging, and filling, it is important to recognize which species are found in estuaries as adults or young. Dependence of the young of marine species on the estuaries is the basis of the nursery ground concept (Gunter, 1967). I expand the nursery ground concept to include all species that are commonly represented by young (defined herein as sexually immature) in estuaries, whether they were spawned in the ocean, estuary, or fresh water.

A total of 168 species is listed for coastal waters (Table 2). The number of species recorded for the estuary is 136 when the numbers of species found only in the freshwater habitat (17) and only along the beach (15) are excluded. The beach and estuary are treated as a single complex here because of their similar fish species compositions. The estuary and beach complex functions as a nursery ground to various degrees for 78 species. Some young sharks and rays that were commonly caught by angling (Dahlberg and Heard, 1969) are included in the compilation. Two species that spawn in fresh water, the anadromous American shad and the white catfish, are also included. The family Sciaenidae includes 13 species that have young dependent on the rich estuarine waters. These sciaenids are the most important group of sport fishes on the Georgia coast and they are potentially important commercial fishes. Atlantic menhaden that are reared in the estuaries are caught offshore in large numbers with purse seines. Vitally important in the food chain are forage species such as the bay anchovy, Atlantic silverside, and rough silverside.

Some organisms that are indigenous to bay or estuarine waters, or at least normally complete their life cycle in these waters, include certain "copepods and planktonic species," several species of molluscs including the American oyster, certain gobioid and cyprinodontid fishes, and a palaemonid shrimp (Gunter, 1967). I have not found fish species that are restricted by salinity tolerances to estuarine waters throughout their

life cycle, but many normally complete their life cycle in the estuary. Some species that typically pass their complete life cycle in the estuary, at least in Georgia estuaries, include those species I later consider to be characteristic of the oyster reefs and certain cyprinodontid fishes such as the marsh killifish, spotfin killifish, and mummichog. The spotted seatrout possibly belongs to this category but adults are common along the beach at times and northern populations migrate offshore in the winter (Tabb, 1966).

There are species that typically complete their life cycle in the ocean or fresh water that are either regular or accidental visitors to the estuary. Another life cycle pattern is exhibited by the anadromous shads (*Alosa*) which spawn in Georgia rivers, including the Altamaha River (Godwin and Adams, 1969). The American eel is the only catadromous species in the estuary.

DIVERSITY OF COASTAL HABITATS

Diversity of habitats is considered here in order to determine the importance of the various habitats to the fish community and also to explore the possible relationship of diversity and stability. A simple index, number of species, is used here in a comparison of habitats (Table 9). To be objective, I define stragglers as those species that are represented by only one collection in a habitat. Further studies would be needed to confidently ascertain which species are naturally rare in their preferred habitats. Discounting stragglers removes a large percentage of the accidental species and makes diversity comparison more meaningful. These diversity values are only roughly comparable because of the differences in sampling effort and gear.

TABLE 9.—Number of species recorded for nine Georgia coastal habitats. To eliminate the influence of stragglers, species recorded (collected or seen) once in the estuary are subtracted from total.

Habitat	Number of species	Species recorded once	Species recorded more than once
1. Beach	114	19	95
2. Lower reach	100	4	96
3. High marsh	56	17	39
4. Middle and upper reaches	61	12	49
5. Oligohaline creek	40	21	19
6. Freshwater creek	39	0	39
7. Tidal canal	22	7	15
8. Low-salinity tidal pool	22	4	18
9. High-salinity tidal pool	37	7	30

The beach habitat produced the highest diversity—114 or 95 species if stragglers are discounted. A high diversity of clupeids, carangids, sciaenids, and bothids accounted for 36 species. Tagatz and Dudley (1961) recorded only 40 fish species from a Beaufort, N.C., beach. Gunter (1958) recorded 44 species from Texas beach station, and Springer and Woodburn (1960) recorded 48 from a beach near Tampa Bay. The latter consider the beach notable for harboring few species compared to other coastal habitats. A low diversity would be expected because the beach offers little niche variety or cover. The higher diversity I report may be attributed to several factors. A large number of species that are typical of other marine and estuarine habitats are occasionally found along the beach. Another factor is the inclusion of eight shark species that were caught while fishing from the beach. A third factor is that Miller and Jorgenson (1969) sampled more extensively than in other studies noted herein. They found 98 species at St. Simons Beach; this total includes 38 species which did not occur at Sapelo Beach.

Species that I consider to be eurythermal in the estuary were collected in both winter and summer and usually in all four seasons, but not necessarily every month. Species that are eurythermal in the beach habitat include the rough silverside (Miller and Jorgenson, 1969), Atlantic silverside, striped killifish, bay anchovy, and striped mullet. Some species that were abundant only in the warm months include the bumper, pompano, white mullet, southern kingfish, and gulf kingfish. Numbers of species and individuals were considerably reduced during the cold months.

The lower reach ranked high in diversity. Most of its 100 species were caught in trawls but seven shark records are based on Dahlberg and Heard (1969). Since only four species are ranked as stragglers, diversity of the characteristic species is similar to the beach habitat. Trawl collections in the region of Cedar Key, Fla., yielded only 63 species (Reid, 1954). This

lower diversity is partially the result of less sampling effort.

Dahlberg and Odum (1970) noted the abundance of species at the 14 trawl stations over the first 14 months of this study. We found that the most numerous species for the first 12 months of the study were star drum (15,209 individuals), weakfish (2,454), blackcheek tonguefish (2,193), sea catfish (1,681), southern kingfish (1,345), silver perch (1,133), bay anchovy (1,090), spot (1,004), Atlantic croaker (896), and spotted hake (467). In shrimp trawl catches in an estuary near Brunswick, 1931-35, Anderson (1968) found the following order of decreasing abundance: star drum, Atlantic croaker, spot, fringed flounder, weakfish, sea catfish, anchovy species, gafftopsail catfish, and kingfish species. In both studies the star drum was the most abundant species. Certain differences (e.g., tonguefish, silver perch, fringed flounder, gafftopsail catfish) may be related to spatial or temporal changes in populations, size of trawl, and mesh size.

Miller and Jorgenson (1969) recorded 56 species, including 39 collected more than once, for the high marsh habitat. Species that were eurythermal in the high marsh also were characteristic of the beach habitat. However, they found the mummichog to be more abundant than the striped killifish in the marsh.

Collections with trawls and seines both contributed heavily to the high diversity (61) of the upper and middle reaches. Some of the species trawled in the middle reach may not occur in the lower salinity upper reach. Species that were eurythermal in the middle reach and common in trawl catches in the middle reach include the Atlantic stingray, bay anchovy, silver perch, spot, southern kingfish, Atlantic croaker, hogchoker, blackcheek tonguefish, and oyster toadfish. Species that were common in trawl catches only during the warm months include the sea catfish, weakfish, star drum, and Atlantic spadefish. Species that were common in trawl catches only during the cold months include the two hake species, spotted seatrout, ocellated flounder, and southern flounder.

Gunter (1967) and others have pointed out that young of marine species are predominant in brackish water. Young fishes that I consider to be eurythermal in the shallow waters (collected by seine, 10-ft trawl, and cast net) of the upper and middle reaches include the Atlantic menhaden, silver perch, spot, southern kingfish, croaker, striped mullet, white mullet, southern flounder, hogchoker, and blackcheek tonguefish. The longnose gar, striped anchovy, bay anchovy, mummichog, tidewater silverside, Atlantic silverside, northern pipefish, and chain pipefish were also characteristic of this region.

The oligohaline section of Riceboro Creek has a low diversity (40 species) especially when the stragglers (21 species) are considered. Tagatz and Dudley (1961) recorded 38 species including 12 freshwater species at an oligohaline station in the Neuse River, N.C. Fishes of the oligohaline creek include 15 freshwater species, 20 euryhaline marine species, 4 anadromous species (*Alosa* and *Dorosoma*), and 1 catadromous species (*Anguilla*). Populations of *Dorosoma* species that occur in saline waters can be considered anadromous as Bailey et al. (1954) have done, but these are primarily freshwater species, at least in Georgia. Characteristic species of the oligohaline creek include the longnose gar, bay anchovy, white catfish, mummichog, mosquitofish, tidewater silverside, bluegill, striped mullet, hogchoker, southern flounder, and spot.

Numbers of fish species decrease up the estuary until the stable freshwater habitat is reached. Most of the 39 species recorded for the freshwater habitat are freshwater species that are characteristic of Coastal Plain waters. Others are migratory or euryhaline marine species, including the anadromous shads (*Alosa*), catadromous American eel, tidewater silverside, northern pipefish, and hogchoker. Fishermen report catching the anadromous striped bass (*Morone saxatilis*) in Riceboro Creek but we have no records.

Miller and Jorgenson (1969) reported 48 species from a freshwater station in the lower Altamaha River. In addition to species that I report, they recorded some marine species, freshwater fishes that usually occur in large rivers and reservoirs, and others that are probably absent from the North Newport River drainage.

The tidal canal and low-salinity tidal pools are

quite similar in diversity and location but some interesting differences exist. The canal is more open to high-salinity water and to the marsh. Larger individuals of some species, such as the striped mullet, silver perch, and spot, entered the canal but not the more isolated pools. The pools contained small species and small individuals of large species. Species characteristic of both habitats include the ladyfish, tarpon, sheepshead minnow, mummichog, mosquitofish, sailfin molly, snook, striped mullet, white mullet, and spot. Species that were restricted to the pools include the marsh killifish, fat sleeper, and freshwater goby.

The greater diversity (37) of the high-salinity tidal pools, compared to the low-salinity pools, is probably related to their higher salinity and greater accessibility from habitats of high diversity (beach and lower reach). As noted previously, salinities and temperatures were similar in the two series of high-salinity pools on the east and west sides of the road to the Sapelo Island lighthouse. Conspicuous faunal differences in the two series of pools may be related to water depth. In the shallow pools of the east side there were large numbers of cyprinodontiform fishes (including the sailfin molly, mummichog, sheepshead minnow, mosquitofish, and striped killifish) and spotfin mojarra. These were all found in much smaller numbers in the deep pool on the west side of the road. The deep pool produced larger numbers of young silver perch, young spot, and gobies. The sharptail goby, emerald goby, and green goby were not found in the shallow pool. Large numbers of striped mullet, white mullet, ladyfish, and bay anchovy were found in the shallow and deep pools.

These semi-isolated tidal pools of estuaries have received little attention in ichthyological studies although they are nursery grounds for many species. Kilby (1955) compared "inner pools" and "outer pools" for two regions on the Florida Gulf coast. He found a higher diversity (36 and 26 species) in the outer pools than in the lower salinity inner pools (19 and 28 species). He did not find significantly more species in open water as I have, because of differences in collecting methods.

The ecological stability of a habitat is generally related to its species diversity. Therefore, it would appear that the low-salinity habitats, tidal pools, and tidal canals would be more vulnerable to pollution than the other habitats. This suggests that locating factories or developments on lower reach or beach habitats would be less likely to damage the fish populations. However, other factors must be considered. For example, the beaches are especially sensitive to development because removal of the stabilizing beach plants results in rapid erosion.

ADDITIONAL COASTAL HABITATS

I consider the oyster habitat to include the oyster reefs of the lower reach and smaller patches of oysters in tidal creeks. The oyster habitat was located near the low tide level and was sampled by hand. Fishes that remain within the interstices between oysters at low tide I consider characteristic. In general order of decreasing abundance, these are: naked goby, feather blenny, skilletfish, seaboard goby, striped blenny, oyster toadfish, and crested blenny. The mummichog was often observed swimming in the vicinity of oysters. At high tide a number of sciaenids migrate to submerged oyster reefs where they provide good fishing. The naked goby, feather blenny, mummichog, and oyster toadfish (one specimen) were also associated with the fouling community on the underside of floating docks in the lower reach.

Few species occur in strictly freshwater habitat on Sapelo Island. Collections were made in a pond at the Marine Institute and ditches at artesian wells. The largemouth bass and bluegill were introduced and are well established in ponds. There are specimens in the University of Georgia Fish Collection of the yellow bullhead and warmouth that were collected on Sapelo Island. These species probably were introduced. Five species that were common in a ditch at an artesian well, locally called Flora Bottom, are the mosquitofish, sailfin molly, marsh killifish, least killifish, and bluefin killifish (*Lucania goodei*). Of these, the first three are euryhaline. The least killifish and bluefin killifish may be native to Sapelo Island, or they could have dis-

persed across the estuary from the mainland since salinities are sometimes reduced to brackish in the estuary.

The stabilization pond of the Interstate Paper Corp. at Riceboro provided a unique study habitat. Fishes were collected on 12 August 1969, 14 April 1970, 2 June 1970, and 6 July 1970. Fishes that were intentionally introduced in 1968 and 1969 and subsequently collected by seining include the largemouth bass, bluegill, and warmouth. Personnel of the paper company also collected adults of the following introduced species: brown bullhead (*Ictalurus nebulosus*) and redear sunfish (*Lepomis microlophus*). I collected four specimens that appeared to be hybrids of the bluegill and redear sunfish. Golden shiners are native to the area but since they were not collected until June and July 1970, they may have been introduced by fishermen. Native species include the mosquitofish, which was abundant, and the least killifish, which was represented by one specimen. I collected juveniles of warmouth, sunfish, mosquitofish, golden shiner, and bass that were spawned in the pond.

DISTRIBUTION PATTERNS OF COASTAL FISHES

The 168 coastal fish species exhibit a variety of distribution patterns in relation to the described habitats. The 86 species that were restricted to one or two habitats included large numbers of (1) freshwater species, (2) elasmobranchs and teleosts that were primarily marine and stenohaline, and (3) rare species. The 30 species that occupied three habitats included only one elasmobranch (*D. sabina*), three freshwater species, and some uncommon and stenohaline species. The large number of species in these categories indicates that a majority of the coastal species occupy only a relatively small number of the coastal habitats. However, the low diversity estuarine habitats (habitats 5, 7, 8, and 9) may be widespread and important nursery grounds to estuarine species that are important as sport, commercial, or forage fishes, e.g., tarpon, anadromous shads, Atlantic menhaden, white catfish, tidewater silverside, silver perch, spotted sea trout, weakfish, spot, Atlantic croaker, striped and white mullets, and southern flounder.

Euryhaline species were defined as species that occur in both fresh water and pure seawater (Gunter, 1956). Although many of the species studied are euryhaline, none were found in all nine habitats. Six species occurred in all habitats except the freshwater habitat, and all of these sometimes occur in fresh water. These widely adapted species are the Atlantic menhaden, mummichog, spotfin mojarra, silver perch, spot, and striped mullet. The mosquitofish, croaker, and white mullet occurred at seven habitats. The mosquitofish was absent from the deepwater habitats. The white mullet and croaker were absent only from low-salinity habitats.

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Mrs. Joyce Swanberg identified representative plants using Radford, Ahles, and Bell (1968) but she used Muenscher (1944) to identify *Elatine*. G. C. Miller identified *Prionotus pectoralis*, now a synonym of *P. salmonicolor*. Dr. C. L. Hubbs identified some *Diapterus olisthostomus*, *Eucinostomus argenteus*, and *E. melanopterus;* Dr. E. Herald, some *Syngnathus fuscus* and *S. louisianae;* Dr. C. R. Gilbert, *Evorthodus lyricus;* and R. W. Heard, Jr., many invertebrates.

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THE RELATIONSHIP BETWEEN THE SUMMER FOOD OF JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, AND THE STANDING STOCK OF ZOOPLANKTON IN ILIAMNA LAKE, ALASKA[1, 2]

STEPHEN H. HOAG[3]

ABSTRACT

The foregut contents of juvenile sockeye salmon in samples taken at night by tow net in the limnetic area of Iliamna Lake consisted primarily of zooplankton and rarely of insects. The number of organisms per foregut was correlated with the estimated zooplankton density between 0 and 100 m. *Cyclops* and *Bosmina* were the dominant zooplankters in both foregut and zooplankton samples. The zooplankton hauls contained a greater percentage of calanoid copepods than the fish foreguts. Food selectivity was indicated but appeared to be minimal. Fry (age 0) foreguts contained a lesser percentage of *Cyclops* and a greater percentage of *Bosmina* than did yearling (age I) foreguts.

Juvenile sockeye salmon (*Oncorhynchus nerka*) spend 1 or 2 years in Iliamna Lake before migrating to sea. They occupy the littoral from the time they emerge from the gravel, in late winter or early spring, until mid-July, when they move to the limnetic area where they remain until migrating to sea in the spring of the following or second year (at age I or age II). A similar change in distribution was found in Lake Aleknagik in the Wood River system (Pella, 1968) and is probably common for all juvenile sockeye salmon in the lakes of Bristol Bay. Preious food studies, summarized by Rogers (1968), indicated that juvenile sockeye salmon feed primarily on insects in the littoral and on zooplankton in the limnetic area.

The standing crop of zooplankton is usually used as an indicator of food availability for zooplankton feeders. However, differences in size, agility, and visibility of the zooplankters may invalidate this assumption.

The objectives of this study were: (1) to determine the food of juvenile sockeye salmon and (2) to compare the composition of the diet with that of the estimated standing stock of zooplankton during the summers of 1966 and 1967. The diets of fry (age 0) and yearlings (age I) were also compared. The population density of juvenile sockeye salmon in Iliamna Lake was high during these years as the escapement into the Kvichak River system was exceptionally large (24.3 million fish) in 1965.

THE ENVIRONMENT

Iliamna Lake is the largest lake in Alaska, with an area of 2,622 km^2 and an average depth of 44 m. It empties into the Kvichak River, which flows into Bristol Bay. The Lake was divided geographically into four sampling areas (Figure 1). Areas I and II have a mean depth of 34 m and an even bottom of glacial till. Area III is much deeper (mean depth 74 m) and has a highly variable, glacially scoured bottom. Area IV is made up of islands and isolated bays and also has a highly variable bottom contour.

Twenty-nine fishes have been identified in the Kvichak River system (Bond and Becker, 1963), but only the sockeye salmon is of commercial importance. The threespine stickleback, *Gasterosteus aculeatus*, the most abundant of the resident species, may compete with the juvenile sockeye salmon for food.

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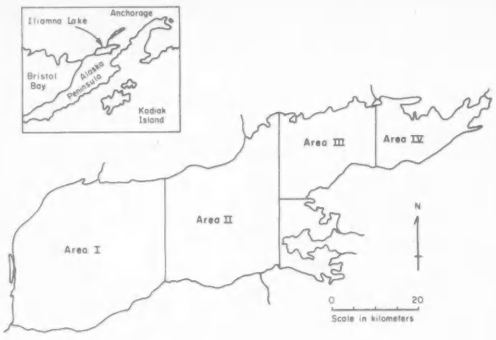

FIGURE 1.—Sampling areas of Iliamna Lake.

The following species of zooplankton occur commonly in the limnetic area of the Lake: *Diaptomus gracilis, Erytemora yukonensis, Cyclops scutifer, Bosmina coregoni, Daphnia longiremis,* and *Holopedium gibberum* (Lenarz, 1966).

Juvenile sockeye salmon and zooplankton exhibit a similar diel vertical migration. Echograms have shown a movement toward the surface at dusk, a concentration usually at less than 10 m at night and a downward movement of fish at dawn. Pella (1968) described a similar diel vertical migration for juvenile sockeye salmon in Lake Aleknagik, Alaska. About half of the zooplankton population occurs above 15 m at midnight and above 50 m at noon in Iliamna Lake (Fowler and Lenarz, 1965).

MATERIALS AND METHODS

Fry (age 0) and yearlings (age I) were collected with a tow net, having an opening of 2.7 m^2 and a cod end mesh size of 0.2 cm, and suspended between two boats spaced 15 m apart with 30.5 m of tow line. Each tow was 20 min in duration at a speed of about 1.5 m/sec. Alternate tows were made at 1.5 and 6 m, and occasionally deeper tows were made when fish were observed at greater depths on the echo sounder. Most samples were taken during darkness (normally between 2100 and 0300 hr). During the day catches were very small at depths of 30 m, and major fish concentrations usually were not seen on the echo sounder. Fishing near the bottom with monofilament, small-meshed gill nets was tried without success.

Fry and yearlings were preserved separately in 10% Formalin within 15 min after capture. No regurgitation of the stomach contents was observed. The fish were measured and the stomachs removed several months later.

The stomach was divided at the major bend, and only the contents of the foregut were examined so that bias from unequal digestive rates among different food items would be minimized. The foregut contents from all the fish in a sample were combined and mixed with water of a known volume. Two subsamples were taken with a 1-ml bulb pipette, and the organisms identified and counted under a low-powered dissecting microscope. Each organism was identified as either *Cyclops, Daphnia, Bosmina, Holopedium,* calanoid copepods, or insects. Nauplii and rotifers were seldom observed and were not counted. The total number of each food item in the sample was estimated by multiplying the number of each food item in the two subsamples by the appropriate factor. The variance between subsamples was less than 1% of the total variance among samples within date and area and was ignored.

The samples ranged from 1 to 45 fish but usually contained between 15 and 25 fish. The results from each sample were weighted by the number of fish per sample and grouped by area and sampling period. The sampling periods were:

1. Late summer 1966 (August 15-September 10).
2. Early summer 1967 (June 20-July 20).
3. Late summer 1967 (August 10-September 5).

The zooplankton sampling (described by Lenarz, 1966) was undertaken for a separate study and differed spatially and temporally from the young fish sampling. Samples were taken with a conical, nylon net of No. 6 mesh attached to a 0.5-m ring by vertical hauls, either from 100 m to the surface or from the bottom to the surface if the depth was less than 100 m. The zooplankters were identified and counted simi-

larly to the organisms in the foregut. Samples were grouped by area and sampling period. The sampling periods were:

1. Late summer 1966 (August 10-26).
2. Early summer 1967 (June 18-30).
3. Late summer 1967 (August 22-September 15).

RESULTS

The numbers of fry and yearlings and the numbers of zooplankton samples by area and sampling period are listed in Table 1. Catches of yearlings in 1966 and of fry in the early summer of 1967 were small and were excluded from the analysis. Both fry and yearlings occurred in varying numbers in nearly all samples during the late summer of 1967. The mean fork length by area and sampling period ranged from 50 to 58 mm for fry and from 71 to 96 mm for yearlings.

TABLE 1.—Summary of samples of fish and zooplankton by area and sampling period.

Sampling period	Area	Age group	Number of fish samples	Number of fish examined	Number of zooplankton samples
Late summer 1966	I	Fry	7	22	9
	II		7	62	9
	III		7	116	6
	IV		17	385	4
Early summer 1967	I	Yearling	7	14	9
	II		8	113	9
	III		7	39	6
	IV		8	81	4
	I	Fry	7	43	9
	II		8	107	9
	III		7	150	6
	IV		7	160	6
Late summer 1967	I	Yearling	8	43	9
	II		8	105	9
	III		7	120	6
	IV		7	90	6
Total			127	1,650	116

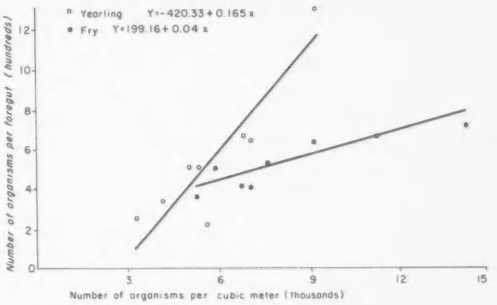

FIGURE 2.—Relationship between the number of organisms per foregut and the number of zooplankton per cubic meter.

FEEDING ACTIVITY

Most juvenile sockeye salmon (94%) contained some food. Temporal and spatial differences in the mean number of organisms in the foregut of juvenile sockeye salmon were apparent although the number of organisms per foregut varied considerably between samples within areas and sampling periods (Table 2). The number of organisms consumed per foregut increased from early to late summer and from area IV to area I.

The mean number of organisms per foregut by age group and the mean number of organisms per cubic meter in each area and sampling period are plotted in Figure 2. The positive slopes, significant at $P = 0.05$, indicate that feeding was in proportion to the abundance of zooplankton. The slope for fry is less than for yearlings probably due to the smaller foregut capacity of fry. Fry probably require a lower food concentration to become satiated, and the number of organisms per foregut may be approaching an

TABLE 2.—Mean number of organisms per foregut and variance between samples by age group, area, and sampling period.

Sampling period	Age group	Area I		Area II		Area III		Area IV	
		$\bar{x}$	s_x^2	$\bar{x}$	s_x^2	$\bar{x}$	s_x^2	$\bar{x}$	s_x^2
Late summer 1966	Fry	715	72,895	685	172,641	525	113,384	502	77,863
Early summer 1967	Yearling	222	46,625	497	157,397	338	8,910	242	50,485
Late summer 1967	Fry	649	66,511	429	31,179	414	20,784	360	35,023
	Yearling	1,323	444,252	680	39,222	660	114,339	496	72,992

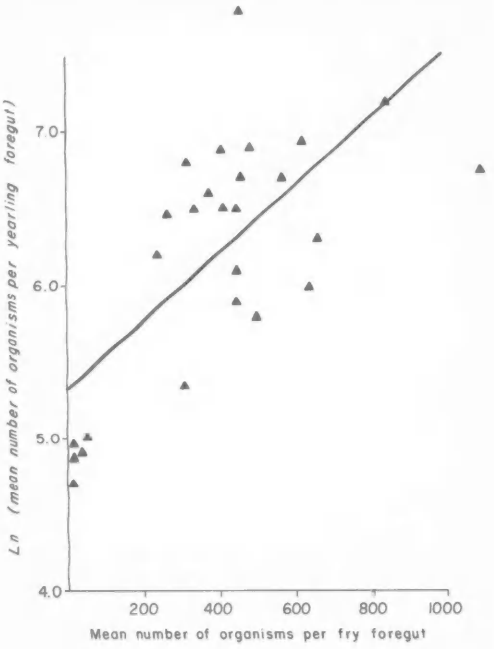

FIGURE 3.—Relationship between the mean number of organisms per foregut in fry and yearlings.

asymptotic upper limit with respect to food abundance in the Lake. The relationship might have been nonlinear for both fry and yearlings if lower and higher zooplankton densities had occurred.

The relationship between the number of organisms per foregut and fish size within each age group was not examined because size range of fry and yearlings in any sampling area was small. However, the yearlings contained an average of 40% more organisms than the fry in the late summer of 1967, probably because of their larger size and feeding capacity. The feeding intensities of both age groups are compared in Figure 3. The correlation coefficient, $r = 0.67$, between the mean number of organisms per fry foregut and the natural logarithm of the mean number of organisms per yearling foregut, significant at $P = 0.05$, indicates an exponential relationship between the feeding intensity of the two age groups. This was expected as fry tend to approach an upper limit of food intake (Figure 2).

COMPOSITION OF THE DIET AND THE ZOOPLANKTON SAMPLES

The food of juvenile sockeye salmon in the limnetic area of Iliamna Lake consisted primarily of zooplankton. Insects averaged less than 1% of the total number of organisms in the foregut except for yearlings from area I during the early summer of 1967, when they constituted 42.6%. *Cyclops* and *Bosmina* were usually dominant in the zooplankton hauls and in the fish foreguts, and averaged 75% in the zooplankton hauls and 90% of zooplankton in the fry and yearling foreguts (Table 3). Yearlings contained a higher percentage of *Cyclops* and a lower percentage of *Bosmina* than fry in late summer 1967 when both age groups were sampled. The percentage of calanoid copepods averaged higher in the zooplankton hauls (13%) than in the fish foreguts (3%) and was consistently higher for all areas and sampling period. *Daphnia* and *Holopedium* occurred in most samples but only constituted 11% of the organisms in the zooplankton hauls and 7% in the fish foreguts.

To compare the percentage composition of organisms in the zooplankton hauls with that of the foregut contents, a "two-way crossed" analysis of variance (fish-zooplankton by area) was performed for each sampling period and for each organism (*Cyclops*, *Bosmina*, and calanoid copepods). *Daphnia* and *Holopedium* were not tested. Mean squares and degrees of freedom are shown in Table 4. The percentage composition of the foregut contents and the zooplankton hauls (Table 3) were significantly different except for *Cyclops* in late summer 1966 and early summer 1967. However, differences in the zooplankton hauls and the foregut contents were not consistent in all areas for *Cyclops* and *Bosmina* as indicated by the significant interaction between the fish-zooplankton samples and areas. Interaction was not significant for the calanoid copepods.

A modification of Tukey's test (Snedecor, 1956, p. 251) showed a significant difference

($P = 0.05$) in the percentage of *Cyclops* and *Bosmina* in fry foreguts, yearling foreguts, and zooplankton hauls in late summer 1967. The percentage of calanoid copepods in fry and yearling foreguts did not differ significantly, but both differed significantly from that in the zooplankton hauls.

Spatial and temporal changes in the composition of the zooplankton catches were compared with changes in the fish foreguts. In the zooplankton hauls, the percentage of *Cyclops* generally decreased and the percentage of *Bosmina* generally increased from early to late summer and from area IV to area I. The composition

TABLE 3.—Mean percentages of *Cyclops*, *Bosmina*, and calanoid copepods in the foregut of fry and yearlings (insects excluded) and in the zooplankton samples by area and sampling period.

Sampling period/ area	*Cyclops*			*Bosmina*			Calanoids		
	Fry	Yearling	Zooplankton	Fry	Yearling	Zooplankton	Fry	Yearling	Zooplankton
	%	%	%	%	%	%	%	%	%
Late summer 1966									
Area I	45.1	--	42.0	45.6	--	38.1	4.0	--	7.1
Area II	29.4	--	41.0	55.5	--	40.9	4.9	--	6.5
Area III	38.1	--	47.5	49.6	--	38.6	1.2	--	6.8
Area IV	26.8	--	62.0	64.5	--	24.9	1.0	--	7.0
Early summer 1967									
Area I	--	58.9	72.4	--	28.9	5.7	--	7.5	13.1
Area II	--	79.0	78.5	--	4.6	3.2	--	1.1	11.0
Area III	--	87.9	84.6	--	4.2	1.2	--	1.7	9.4
Area IV	--	92.3	77.8	--	1.8	1.0	--	4.5	17.9
Late summer 1967									
Area I	21.0	47.2	27.5	68.3	44.0	34.6	2.5	2.3	17.0
Area II	34.6	54.7	14.0	54.3	34.4	45.7	2.3	2.4	16.4
Area III	75.2	84.8	38.4	18.2	6.8	27.0	2.8	2.6	21.1
Area IV	77.6	84.7	36.1	18.0	9.9	23.5	2.3	3.7	24.0
All sampling periods/area	43.5	73.6	51.8	46.8	16.8	23.7	2.6	3.2	13.1

TABLE 4.—Mean squares and degrees of freedom for a "two-way crossed" analysis of variance by sampling period and zooplankton.

	Cyclops		*Bosmina*		Calanoids	
	Mean square	Degrees of freedom	Mean square	Degrees of freedom	Mean square	Degrees of freedom
Late Summer 1966						
Treatments (zooplankton, fry)	65.9	1	644.3**	1	33.0**	1
Areas	117.4**	3	14.0	3	1.5	3
Interaction (treatment × area)	127.7**	3	106.8*	3	1.6	3
Residual	20.6	58	28.1	58	.6	58
Early summer 1967						
Treatments (zooplankton, yearlings)	3.4	1	100.7**	1	166.6**	1
Areas	178.6**	3	109.2**	3	16.8*	3
Interaction (treatment × area)	67.8	3	57.2**	3	5.8	3
Residual	30.8	50	10.6	50	4.8	50
Late summer 1967						
Treatments (zooplankton, fry, yearlings)	1,514.5**	2	615.0**	2	386.1**	2
Areas	1,086.8**	3	887.5**	3	6.0	3
Interaction (treatment × area)	121.0**	6	97.5**	6	3.5	6
Residual	26.9	77	25.0	77	3.5	77

* F test significant at $P = 0.05$.
** F test significant at $P = 0.01$.

TABLE 5.—Rank correlation coefficient (r_d) for percentage of five organisms in fish foreguts and zooplankton hauls by area and sampling period.

Sampling period	Samples	Area			
		I	II	III	IV
Late summer 1966	Fry-zooplankton	0.975***	0.975***	0.800*	0.800*
Early summer 1967	Yearling-zooplankton	.675	.425	.300	.700
Late summer 1967	Fry-zooplankton	.700	.225	.900**	1.00***
	Yearling-zooplankton	.600	−.025	.825*	1.00***

* Significant at $P = 0.20$.
** Significant at $P = 0.10$.
*** Significant at $P = 0.05$.

of organisms in the yearling foreguts showed a similar change; for *Cyclops* and *Bosmina* $r = 0.66$ (significant at $P = 0.10$) and 0.71 (significant at $P = 0.05$), respectively. Correlation was not significant for fry ($r = 0.01$ and 0.22, respectively). The percentage of calanoid copepods in the fish foreguts remained constant in spite of an increase from early to late summer in the zooplankton hauls (Table 3).

Although differences were significant in the percentage composition of organisms in the zooplankton hauls and in the fish foreguts, the fish fed predominantly on those organisms which were most abundant in the zooplankton hauls. Rank correlation coefficients (r_d) were used in comparing the percentage of *Cyclops*, *Bosmina*, calanoid copepods, *Daphnia*, and *Holopedium* in the zooplankton hauls and in the foreguts, and showed very good correlation in several areas and sampling periods and, with one exception, were always positive (Table 5).

COMPARISON OF FRY AND YEARLING DIETS

Cyclops and *Bosmina* were the major food items in the diet of both fry and yearlings although the percentage of the former was greater and the percentage of the latter smaller in the yearling foreguts than in the fry foreguts (Table 3). Differences in the foregut contents may result from slight differences in habitat and hence from differences in available food.

To minimize this possibility only those samples that included at least five fry and five yearlings were examined. The relationship between the two age groups in the percentage of *Cyclops* and *Bosmina* in the foreguts appeared linear (Figures 4 and 5) and a regression analysis was performed. The slope (b) was significantly greater than zero ($P = 0.05$) for both zooplankters; thus, the two age groups have similar food habits. However, the hypothesis $b = 1$ was rejected ($P = 0.05$); therefore, I concluded that fry consume more *Bosmina* and less *Cyclops* than yearlings. The positive intercept in Figure 4 and b less than 1 in Figures 4 and 5 indicate that the percentage of *Cyclops* and *Bosmina* vary less in yearling than in fry foreguts.

DISCUSSION AND CONCLUSIONS

Cyclops and *Bosmina* were the most abundant, and calanoid copepods, *Daphnia*, and *Holopedium*, the least abundant zooplankters in the fish foreguts and in the zooplankton hauls. However, the percentage composition of organisms in fish foreguts differed significantly from those in the zooplankton hauls in that: fry contained more *Bosmina;* yearlings contained more *Cyclops;* fry and yearlings contained less calanoid copepods than the zooplankton hauls.

Discrepancies in estimates of available food and diet are due to sampling error and selective feeding. Spatial and temporal differences in the sampling of zooplankton and fish, and diel and depth variations in available food and feeding activity probably accounted for some discrepancy. Fowler and Lenarz (1965) established diel and depth variations in the percentage composition of the standing zooplankton stock in the lake. Northcote and Lorz (1966) showed diel changes in the food of resident sockeye salmon (kokanee) in Nicola Lake, British Columbia,

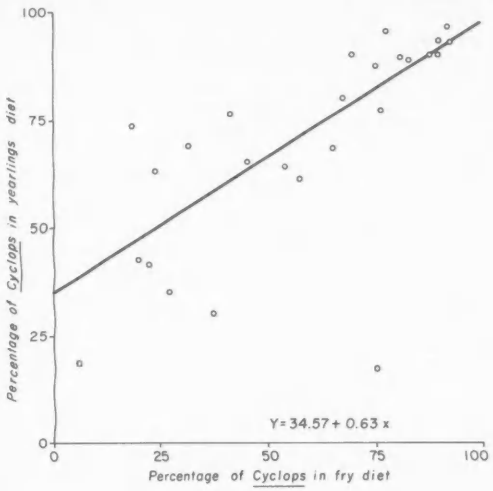

FIGURE 4.—*Relationship between the percentage of Cyclops* in the foregut of fry and yearlings.

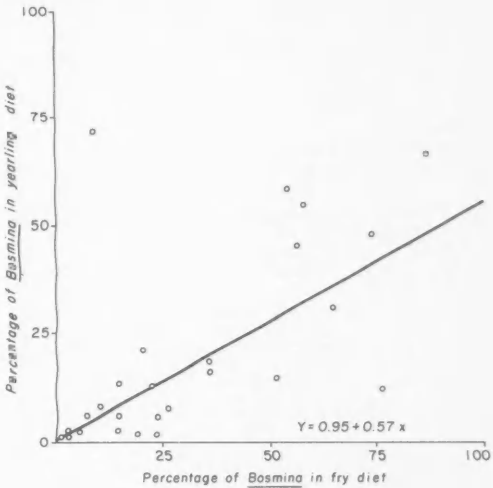

FIGURE 5.—*Relationship between the percentage of Bosmina* in the foregut of fry and yearlings.

and Narver (1970) showed diel and depth changes in the food of juvenile sockeye salmon in Babine Lake, British Columbia.

Food selection depends on characteristics of the feeder and food items (Ivlev, 1961) and probably occurs in some degree for all species. In this study, the cause of the discrepancy between the composition of the foregut and zooplankton samples cannot be attributed specifically either to sampling error or to selective feeding. Whatever the cause, the degree of discrepancy was small, and I concluded that the zooplankton samples generally reflect available food in Iliamna Lake. This is in contrast to Narver (1970), who found that juvenile sockeye salmon strongly selected numerically less abundant zooplankters in Babine Lake.

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SMALL-SCALE DISTRIBUTIONS OF OCEANIC DIATOMS

E. L. VENRICK[1]

ABSTRACT

A sampling study was designed to investigate small-scale abundance fluctuations of diatoms over a distance of 10 miles. It was carried out at three depths in each of two oceanic environments of the North Pacific. Significant nonrandom distributions were observed. The intensity of aggregation varied with species and with depth.

An expression for the approximate confidence intervals for single observations was derived from the 5th and 95th percentiles of the observed frequency distributions.

Statistical analysis of the fluctuations of *Nitzschia turgiduloides* indicated a pattern of distribution with a scale of 1 mile. This may be associated with internal waves in the region of the thermocline.

Knowledge of small-scale distributions of organisms in the ocean is important for evaluation of data based on widely spaced samples, and, hence, is essential for design of efficient sampling programs. Moreover, abundance fluctuations on even the smallest scale relate directly to the ecology of the species, and an understanding of the magnitude and scale of such fluctuations is an important step toward the understanding of a species' relationship to its environment and to other species within its community.

Evidence indicates that the distribution of phytoplankton in the ocean may be highly aggregated (Bainbridge, 1957). A few attempts have been made to sample small-scale aggregations and to investigate quantitatively their density and spacing and the environmental factors which influence them (e.g., Hasle, 1954; Holmes and Widrig, 1956; Barnes and Hasle, 1957; Cassie, 1959a, b, 1960; Bernhard and Rampi, 1965). Although these studies applied a wide variety of statistical procedures to a range of spatial and temporal scales, all of the phytoplankton species studied were reported to have aggregated distributions. However, such studies have all been conducted in the nearshore environments. If, as has been suggested (Cassie, 1957), the contagious distributions of plankton reflect heterogeneities in the environment, then the results of such studies may not be applicable to the more homogeneous environments of the open ocean.

The study described in this paper was carried out in two oceanic environments of the North Pacific. While it was primarily designed to give a quantitative estimate of the precision of samples collected for an extensive study of oceanic diatoms, the results have general interest.

LOCATION OF STUDY

Closely spaced samples were taken twice during Scripps Institution of Oceanography Expedition URSA MAJOR, August-September, 1964. Station 23 (lat 49°07'N, long 155°31'W) was located in the Central Subarctic Pacific and Station 5 (lat 37°00'N, long 155°02'W) in the Central Pacific (Dodimead, Favorite, and Hirano, 1963); both regions were removed from the effects of either neritic environments or the North Pacific Transition Domain. The phytoplankton of the Central Subarctic consisted primarily of diatoms which reached densities in excess of 5,000 cells/100 ml. A total of 27 diatom species was recorded, of which *Nitzschia turgiduloides* comprised 68-92% of the population, and *Denticula seminae* an additional 9-20%. The maximum density of diatoms at the Central Pacific station was only 30 cells/100 ml. The dominant species, *Hemiaulus hauckii*, contributed 20% of the

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total diatom population, and 16 additional species were recorded. Subsequent samples from this region indicated that the major diatom population was below the depth range of the sampling study.

METHODS

At each location a line of stations was positioned with respect to a 10-m drogue. In the Subarctic Pacific, 10 stations were sampled; in the Central Pacific, 11. The stations were spaced at randomly ordered intervals of 0.5, 1.0, and 2.0 nautical miles, covering a total distance of 10.5 miles. At each station samples were collected from depths of 10, 35, and 50 m (wire out).

Samples were collected with 3-liter Van Dorn water samplers. The organisms in samples of 400 ml were preserved with 10 ml of 10% basic Formalin. Aliquots of 50 or 100 ml were settled for 24 hr and the diatoms identified and enumerated under the inverted microscope according to the sedimentation procedure of Utermöhl (1931). The species used for the analysis of distributions were those for which experience has shown the problems of identification and enumeration are negligible. In the case of chain-forming species, the statistical analyses were based upon the numbers of chains per aliquot.

STATISTICAL PROCEDURES

The variance of the cell counts includes the variability introduced into the data during the preparation and enumeration of the subsample, as well as any spatial heterogeneity. If these are independent, the sums of squares will be additive:

$$SS_{total} = SS_{subsample} + SS_{spatial}$$

and the total observed variance is given by:

$$s^2_{total} = SS_{total}/\text{degrees of freedom}.$$

In a brief preliminary study it was demonstrated that, for all species but one, the variability introduced into the data at either the initial or final subsampling stage was no greater than random (Poisson) expectation and may be approximated by the mean count. This agrees with the results of other workers (Holmes and Widrig, 1956; Lund, Kipling, and Le Cren, 1958). The single exception was *Nitzschia turgiduloides*, for which the total introduced variability was $35\bar{X}$.

It has been shown (Venrick, 1971) that the expected total variance of a series of counts from a randomly distributed population is given by:

$$\sigma^2 = \Big\{(n_{al}-1)\,(n_{ss})\,(n_{pop})\,(1-\frac{1}{f_1})\,\bar{X}_{al} + [\,(n_{ss}-1)\,(n_{pop})\,(1-\frac{1}{f_2}) \times (\bar{X}_{al} + \frac{n_{al}}{f_2}\bar{X}_{al})\,] + (n_{pop}-1)\,[\bar{X}_{al} + \frac{n_{al}}{f_2}\bar{X}_{al} + \frac{n_{al}\,n_{ss}}{f_1\,f_2}\bar{X}_{al}]\Big\}/[n_{al})\,(n_{ss})\,(n_{pop}) - 1]$$

where n_{al}, n_{ss}, and n_{pop} are the numbers of aliquots per subsample, the numbers of subsamples per sample, and the number of samples collected from each depth; f_1 is the ratio of sample volume to subsample volume, f_2 is the ratio of subsample volume to aliquot volume; and $\bar{X}_{al}$ is the mean number of cells (or chains) per aliquot. Substituting $n_{al} = 1$, $n_{ss} = 1$, and $f_1 = \frac{3000}{400} = 7.5$, the expression simplifies to:

$$\sigma^2 = \bar{X}_{al} + \frac{1}{f_2}\bar{X}_{al} + \frac{1}{7.5\,f_2}\bar{X}_{al},$$

where $f_2 = 8.0$ for 50 ml aliquots and 4.0 for 100 ml aliquots. For *N. turgiduloides*, the appropriate expected variance is:

$$\sigma^2 = 35\bar{X}_{al} + \frac{1}{7.5\,f_2}\bar{X}_{al}.$$

At each depth, the observed variance, s^2, may be compared with the expected variance, σ^2, and the probability of departure from random expectation determined by means of the ratio

$s^2/\sigma^2 = \chi^2/df$. For 10 and 11 samples $\chi^2(0.05)/df$ values are 1.88 and 1.83 respectively. Species for which the s^2/σ^2 ratio exceeds the χ^2/df value are considered to have aggregated distributions. Ratios greater than 1.63 and 1.60 respectively were significant at the 0.10 level.

With the small number of degrees of freedom involved, the maximum variance attainable by species with mean counts less than 0.2 is too small to give an s^2/σ^2 ratio significant at better than the 0.10 level. For rarer species, a runs test on presence and absence (Tate and Clelland, 1959) was used to give additional information about distribution patterns.

RESULTS

The detection of aggregation in a population is influenced by interaction between volume and spacing of field samples and the scale of aggregation of the population (Grieg-Smith, 1964), and by the proportion of the initial sample which is ultimately enumerated (Venrick, 1971). Thus, the specific results of this study are strictly pertinent only to this sampling design, and they must be interpreted accordingly.

The results of these studies are presented in Tables 1 and 2. Within the Subarctic region, 8 of the 24 distributions were significantly aggregated at the 0.05 level, and two additional species at the 0.10 level. At every depth the species with contagious distributions were the most abundant ones, with the exception of *N. turgiduloides* at 10 m. It is likely that spatial variability of this species was obscured by the large sampling error. Aggregations of the dominant species would result if they had outgrown, in situ, the other species. The fewest aggregated distributions occurred at 10 m. This was the only sampled depth within the mixed layer, and presumably, wind-driven turbulence was sufficient to keep all but the most rapidly dividing species distributed randomly.

Within the Central Pacific, only 3 of the 20 distributions were significantly nonrandom, at the 0.05 level. The runs test, significant at the 0.10 level, indicated that five additional species were aggregated. In this region, aggregation did not appear to be related to the abundance of the species.

Concordance tests were used to investigate the agreement of species with respect to fluctuations of abundances between samples. At Subarctic Station 23 there was significant concordance ($P < 0.05$) between all species at each of the three depths, indicating that species tended to respond to, or be influenced by, their environment in the same manner. In contrast, there was no concordance between species at any depth at Central Pacific Station 5.

PRECISION OF SINGLE SAMPLES

ESTIMATES OF ABUNDANCE

If the frequency distribution of organisms in the field can be fitted to a theoretical distribution, confidence limits on single observations can be derived from the variance of that distribution. Some workers (e.g., Winsor and Clarke, 1940; Barnes and Hasle, 1957) have successfully used logarithmic transformations to normalize abundance data. This procedure was successful for some of the diatom species under consideration in this study. (Normality was tested with normal-probability paper.) The transformation, however, was not successful for all species at all depths and thus a general use of parametric statistics on log-transformed data was not justifiable.

The observed frequency distributions of the aggregated species were satisfactorily predicted by the negative binomial distribution (Anscombe, 1949). Values of k (estimated from the expression $k = \bar{X}^2/(s^2 - \bar{X})$ for the aggregated species ranged from 0.15 to 13.30. The comparisons between the predicted and the observed cumulative frequency distributions were made with Kolmogorov-Smirnov tests (Tate and Clelland, 1959); none were significantly different at the 0.10 level. There are available transformations which normalize negative binomial distributions (Anscombe, 1948). However, these transformations depend upon knowledge of the value of k and thus are applicable only to this particular set of data and not to observations of other species or observations from other environments.

TABLE 1.—Results of sampling study at Subarctic Pacific Station 23.

Species	$\bar{X}_{al}$	σ^2	s^2	s^2/σ^2	P
I. 10-m depth					
Nitzschia turgiduloides[1]	513.5	17,981.23	20,764.30	1.15	--
Denticula seminae[1]	53.8	61.44	271.28	4.42	<0.001
Chaetoceros atlanticus[1]	8.4	9.59	8.26	0.86	--
Dactyliosolen mediterraneus[1]	4.4	5.02	9.30	1.85	<0.10
Coscinodiscus marginatus	2.1	2.40	0.76	0.32	--
Rhizosolenia alata[1]	1.6	1.83	2.26	1.23	--
Thalassiothrix longissima	1.5	1.71	1.16	0.68	--
Rhizosolenia hebetata hiemalis	1.3	1.48	1.56	1.05	--
Corethron criophilum	1.1	1.26	0.98	0.78	--
II. 35-m depth					
Nitzschia turgiduloides[1]	801.0	28,048.62	122,374.22	4.36	<0.001
Denticula seminae[1]	119.3	136.24	1,966.23	14.43	<0.001
Dactyliosolen mediterraneus[1]	23.1	26.38	367.11	13.92	<0.001
Chaetoceros atlanticus[1]	3.0	3.43	17.55	5.12	<0.001
Thalassiothrix longissima	1.5	1.71	3.16	1.85	<0.10
Rhizosolenia hebetata hiemalis	1.4	1.60	2.04	1.28	--
Rhizosolenia alata[1]	0.9	1.03	0.76	0.74	--
Corethron criophilum	0.9	1.03	0.98	0.95	--
Coscinodiscus marginatus	0.8	0.91	1.28	1.41	--
III. 50-m depth					
Nitzschia turgiduloides[1]	330.6	11,581.91	291,104.04	25.13	<0.001
Denticula seminae[1]	39.0	50.04	279.33	5.58	<0.001
Dactyliosolen mediterraneus[1]	7.7	9.88	65.30	6.61	<0.001
Corethron criophilum	0.7	0.90	1.13	1.26	--
Coscinodiscus marginatus	0.6	0.77	0.93	1.21	--
Chaetoceros atlanticus[1]	0.2	0.26	0.40	1.54	--
Rhizosolenia hebetata hiemalis	0.1	0.13	0.10	0.77	--

[1] Statistics based on numbers of chains per aliquot.

The expression which was ultimately chosen to estimate the precision of single observations was derived empirically from the 5th and 95th percentiles of the frequency distributions. For any single count, x, of a nonrandomly distributed species at a single depth, it was found that the expression

$$0.3x \leqslant \bar{X} \leqslant 3.2x$$

included the observed population mean X 90% of the time. The expression was conservative for species with nonaggregated distributions. When all species were considered, the expression included the population mean 95% of the time. The expression gave satisfactory results for estimates of mean numbers of cells of chain-forming species ($P \sim 0.13$) and for mean total diatom abundances ($P \sim 0.14$).

The use of this expression is demonstrated in Table 3, where it has been applied to two samples from 35-m depth at Subarctic Station 23.

TABLE 2.—Results of sampling study at Central Pacific Station 5.

Species	$\bar{X}_{al}$	σ^2	s^2	s^2/σ^2	P
I. 10-m depth					
Hemiaulus hauckii[1]	2.4	3.08	3.45	1.12	--
Asterolampra marylandica	1.0	1.28	1.00	0.78	<0.10 (r)
Rhizoselenia hebetata semispina[1]	0.7	0.90	3.42	3.80	<0.001
Asteromphalus heptactis	0.4	0.51	0.45	0.88	--
Chaetoceros dadayi[1]	0.4	0.51	0.45	0.88	<0.10 (r)
Nitzschia sicula	0.3	0.38	0.21	0.55	--
Mastogloia rostrata	0.3	0.38	0.41	1.08	--
II. 35-m depth					
Hemiaulus hauckii[1]	1.2	1.54	4.56	2.96	=0.001
Nitzschia sicula	0.7	0.90	0.42	0.47	<0.10 (r)
Asteromphalus heptactis	0.6	0.77	0.45	0.58	-
Mastogloia rostrata	0.4	0.51	0.27	0.53	<0.10 (r)
Bacteriastrum sp.[1]	0.4	0.51	1.45	2.84	<0.01
Chaetoceros bacteriastroides var.	0.4	0.51	0.45	0.88	--
Chaetoceros bacteriastroides	0.4	0.51	0.45	0.88	--
Asterolampra marylandica	0.1	0.13	0.09	0.69	--
Chaetoceros dadayi[1]	0.1	0.13	0.09	0.69	--
III. 50-m depth					
Nitzschia sicula	0.9	1.15	1.70	1.48	--
Hemiaulus hauckii[1]	0.8	1.03	1.17	1.14	<0.10 (r)
Chaetoceros bacteriastroides[1]	0.4	0.51	0.27	0.53	--
Asteromphalus heptactis	0.2	0.26	0.16	0.62	--
Bacteriastrum sp.[1]	0.2	0.26	0.16	0.62	--
Chaetoceros bacteriastroides var.	0.2	0.26	0.16	0.62	--
Asterolampra marylandica	0.1	0.13	0.09	0.69	--
Mastogloia rostrata	0.1	0.13	0.09	0.69	--

[1] Statistics based on numbers of chains per aliquot.
r Nonrandomness indicated only by runs test.

For the more abundant species, the 95% confidence limits which can be placed around a single sample are extremely broad. However, without replicate samples, this interval cannot be significantly reduced. For species represented in a sample by fewer than five cells, the confidence interval given by the empirically derived expression is smaller than that obtained from the assumption of a Poisson distribution. For these rarer species, it is recommended that the confidence interval around a single sample be derived from the assumption of a Poisson distribution (Fisher and Yates, 1957).

ESTIMATES OF DIVERSITY

The variability of individual species in the field determines the precision with which a

single sample estimates the structure of the assemblage. The phytoplankton association within the Subarctic Pacific had a low diversity and significant concordance between species. As a result, the species showed a high degree of consistency of relative abundances within samples. In every sample *Nitzschia turgiduloides* was the numerically dominant species, *Denticula seminae* was the second dominant, and one of two species, *Chaetoceros atlanticus* or *Dactyliosolen mediterraneus* was third in abundance. Thus, a single sample appeared to give a precise estimate of the structure of a less diverse assemblage, even though the large between-sample variability decreased the precision of the estimate of absolute abundances of single species.

In contrast, the phytoplankton association in the upper 50 m of the Central Pacific had a high diversity and lacked concordance between species. At 10, 35, and 50 m, respectively, three, seven, and five species were dominant in at least one sample. Thus, a single sample from a diverse assemblage gave an imprecise estimate of the relative abundances of the component species.

TABLE 3.—Confidence interval about single samples. (95% confidence intervals about single samples, x, calculated from the expression $0.3x - 3.2x$ and compared with the population mean density as estimated by the mean of 10 samples, $\bar{X}$.)

Species		$\bar{X}$	Substation e[1]		Substation h[1]	
			x	Confidence interval	x	Confidence interval
Station 23, 35 m; 50-ml aliquots						
Nitzschia turgiduloides	cells	3,018.0	1,481	444.3-4,739.2	4,654	1,396.2-14,892.8
	chains	801.0	484	145.2-1,548.8	1,252	375.6- 4,006.4
Denticula seminae	cells	395.8	175	52.5- 560.0	624	187.2- 1,996.8
	chains	119.3	87	26.1- 278.4	169	50.7- 540.8
Dactyliosolen mediterraneus	chains	23.1	8	2.4- 25.6	64	19.2- 204.8
Chaetoceros atlanticus	cells	7.7	3	0.9- 9.6	25	7.5- 80.0
	chains	3.0	1	0.3- 3.2	11	3.3- 35.2
Rhizosolenia hebetata hiemalis	cells	1.6	0	-- --	3	0.9- 9.6
	chains	1.4	0	-- --	2	0.6- 6.4
Thalassiothrix longissima	cells	1.5	2	0.6- 6.4	1	0.3- 3.2
Corethron criophilum	cells	0.9	1	0.3- 3.2	1	0.3- 3.2
Total cells		3,491.1	1,704	511.2-5,452.8	5,445	1,633.5-17,424.0

[1] Substations e and h separated by 3.5 nautical miles.

ANALYSIS OF PATTERNS

In the analysis of patchiness and its causal factors, the size and shape of a patch often receives primary consideration. This approach is hampered by the difficulty of accurately defining a patch, particularly where, as in the ocean, one can rarely see the patch as a physical entity. An alternate approach is to examine the scale on which a population shows consistent spatial distribution, regardless of the degree of contagion. Since the detection of nonrandomness depends upon the interaction of the size and distribution of the samples with the population distribution, if the scale of sampling is systematically altered, the observed population variance may change, and those sampling scales which produce maximum variances may indicate scales of heterogeneity in the population distribution.

The six sets of 10 and 11 samples were considered as sets of 45 and 55 pairs of samples separated by intervals of 0.5, 1.0, 1.5, . . . 10.5 miles. For all nonrandomly distributed species, the variance was calculated between each possible pair of samples and averaged for each interval. Thus, for the set of 10 Subarctic samples, in which three pairs were separated by 0.5 mile, four pairs by 1.0 mile, two pairs by 1.5 miles, etc., $\bar{s}^2_{0.5}$ is an average of three variances, $\bar{s}^2_{1.0}$ an average of four variances, $\bar{s}^2_{1.5}$ an aver-

age of two variances, etc. The average variances were plotted against the sampling interval, i.

In the case of one species, *N. turgiduloides*, this technique revealed a periodicity of $\bar{s}_i^2$ with peaks separated by 1-mile increments of the sampling interval (Figure 1 b-d). This indicates a pattern of heterogeneity on a scale of 1 mile which was not apparent from a direct plot of abundances (Figure 1a). The periodicity was best developed at 35 m (runs test significant at $P < 0.001$) where it centered about the population variance, as measured by the total variance of the 10 samples. The periodicity was also highly significant (runs test, $P = 0.01$) at 10-m depth. At 50 m the variance showed significant periodicity ($P = 0.10$) only when the sample from substation h was omitted from the calculation. The high population densities of *N. turgiduloides*, and other species, encountered at substation h were comparable to densities observed at shallower depths, and may represent another scale of patchiness imposed upon the deeper populations by vertical mixing.

The horizontal pattern observed in *N. turgiduloides* was most highly developed along the top of the seasonal thermocline, which, at Station 23, extended between 30 and 50 m. Internal waves travelling along the thermocline produce a regular series of vertical displacements, which may occur on a scale of 1 mile. In species with strong vertical gradients of density at the top of the thermocline, such circulation patterns would produce regular horizontal fluctuations of abundance, such as were observed in the present study. The effect of vertical displacement on the less strongly stratified species may have been obscured by their horizontal variations.

This technique has been successfully used to investigate patterns of terrestrial vegetation (Grieg-Smith, 1964). Once scales of heterogeneity have been defined, those environmental parameters that vary on scales of similar magnitude may be sought as possible determinants of the species patterns. Because this approach is not limited to factors which can be measured simultaneously, it is very flexible. It is applicable not only to parameters in effect at the time of sampling, but also to those whose effect on phytoplankton was exerted some time in the past, and which cannot therefore be directly correlated with abundance. It may for instance prove to be a useful tool for examining the effect of vertically migrating herbivores on the standing stock of phytoplankton.

SUMMARY AND CONCLUSIONS

Of the distributions examined in the present study, less than half showed significant aggregation. For these species the 90% confidence interval about a single sample, x, could be estimated from the interval $0.3x$ — $3.2x$. This expression was conservative for the nonaggregated species.

The inability to establish contagion for the majority of the species investigated in the present study does not prove randomness on this or other scales. However, the prevalence of nonaggregated distributions lends support to the hypothesis that the oceanic environment is less complex than that of the nearshore region. In the oceanic environment, the numerous processes which bring about local variations in abundance of phytoplankton appear to proceed more slowly relative to the randomizing turbulent processes. In such an environment, only the most important local processes produce a measureable effect, and, thus, these may be relatively easily isolated for further study.

ACKNOWLEDGMENTS

I am grateful to Professor E. W. Fager for his help with the statistical analysis, and for his criticism of the first draft of this paper.

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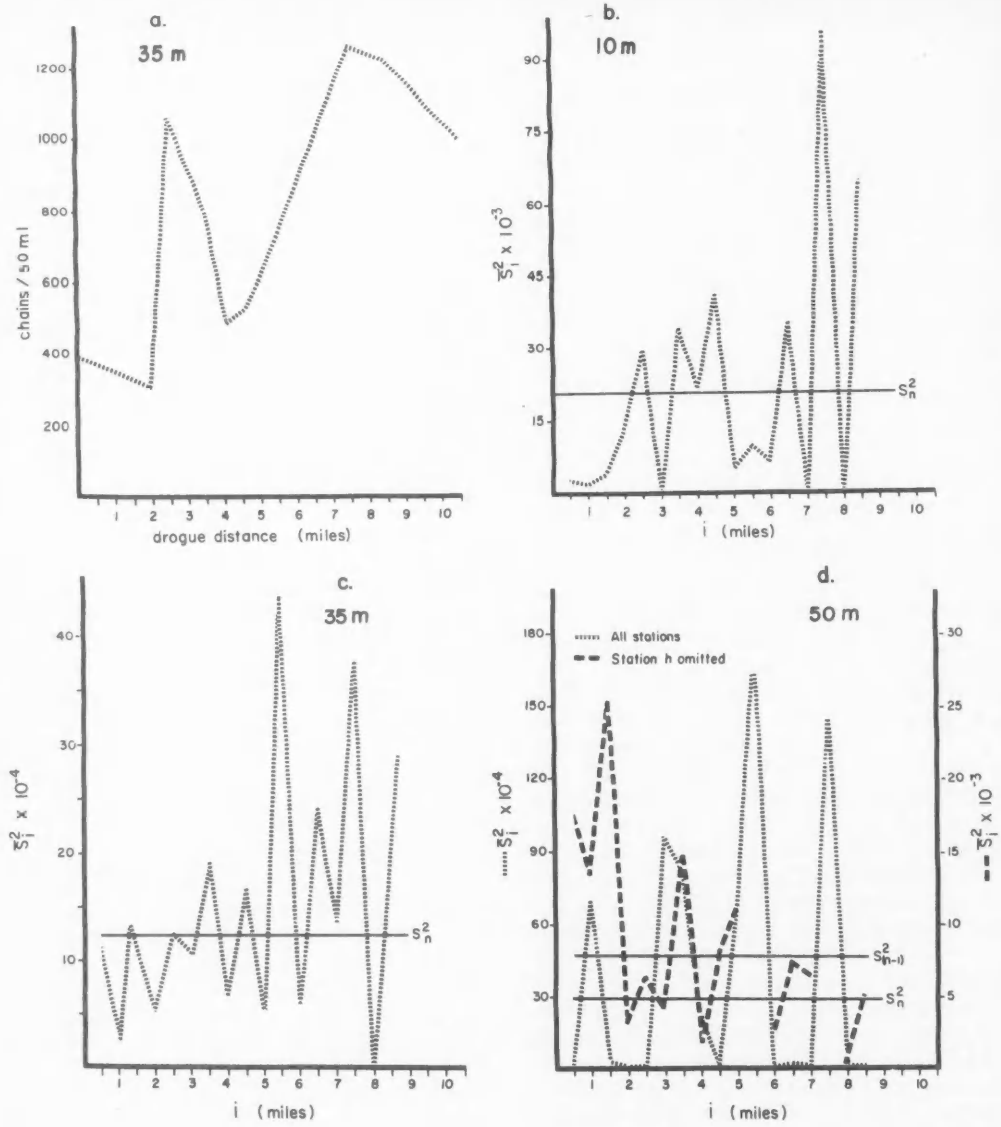

FIGURE 1.—Small-scale distribution patterns of *Nitzschia turgiduloides*. (a) Fluctuations in the abundance of chains, 35 m. (b-d) Fluctuations of the mean, two-sample variance, $\bar{s}_i^2$, with increasing sample interval, i, compared with total variance, s_n^2, of 10 samples: (b) 10 m; (c) 35 m; (d) 50 m; analysis run with (dotted line) and without (dashed line) substation h.

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LABORATORY OBSERVATIONS ON THE EARLY GROWTH OF THE ABALONE, *HALIOTIS SORENSENI*, AND THE EFFECT OF TEMPERATURE ON LARVAL DEVELOPMENT AND SETTLING SUCCESS

DAVID L. LEIGHTON[1]

ABSTRACT

The influence of temperature on larval development rate and growth of juveniles of the white or Sorensen's abalone, *Haliotis sorenseni*, was investigated using a thermal gradient apparatus. *While larvae developed most rapidly at 20°C, most settled juveniles at that* temperature did not survive. At 15-16°C, however, the operculate veliger stage was attained in 72 hr and settlement of advanced individuals occurred in 9 days. No settling was observed at 10°C. Juveniles maintained at 15-19°C and provided mixed diatoms as food showed marked variability in growth rate; at 130 days shell length ranged from 4.0 to 8.0 mm (average 5.5 mm). *Two distinctly different patterns of shell pigment* distribution emerged with continued growth. Approximately 60% of the juveniles were *bicolored, red and yellow-green, while the remainder had an even tone of red-violet.*

The description by Carlisle (1962) of the trochophore and early veliger stages of the red abalone, *Haliotis rufescens* Swainson, has heretofore been the only published information on larval development of an eastern Pacific species of *Haliotis*. No account of larval development through settlement and juvenile growth of any of the seven American species of abalones exists in the literature. Details of larval morphogenesis and an estimate of growth during the first year of life for the northeastern Atlantic *H. tuberculata* Linnaeus were given by Crofts (1929, 1937). Japanese workers have reported observations on early development and growth in several of their native species; *H. gigantea* Chemnitz (Murayama, 1935), *H. discus* Reeve and *H. sieboldii* Reeve (Ino, 1952), and *H. diversicolor supertexta* Lischke (Ōba, 1964).

Recent interest in mass culture of commercially important species in Japan and the United States has prompted more critical studies of growth and nutrition of abalones. Advances by Japanese workers in the field of abalone culture were reported by Imai (1967) and Ryther (1968). However, no comparable research information has been published heretofore from any abalone culture facility in California. This work, done in conjunction with abalone culture efforts of California Marine Associates, Cayucos, Calif., describes early growth of the white or Sorensen's abalone, *Haliotis sorenseni* Bartsch.

H. sorenseni exhibits an unusual pattern of distribution. Common to southern California and northern Baja California, it appears in abundance along the mainland only at the northern and southern extremes of its range (Santa Barbara to Pt. Conception and Pta. Eugenia to Pta. Abreojos, respectively). Elsewhere it is islandic, occurring at Santa Cruz, Santa Barbara, San Clemente, Santa Catalina, Los Coronados, and Cedros Islands (Cox, 1962). Adults attain a shell length of about 25 cm and are characterized by an orange-tan epipodium with foliose epipodial papillae, brown cephalic tentacles, and a deeply cupped, light-weight, and scar-free shell. Respiratory apertures are strongly fluted. The species is prized by commercial and sport divers for its white and tender edible portion, the right shell muscle.

Sexually mature *H. sorenseni* have been difficult to obtain in good condition since this is a relatively fragile species and losses in transit

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have been common. On several occasions gravid adults have been retained in our tanks and induced to spawn, but such attempts were never successful in obtaining their larvae. It is considered, therefore, of importance to document a first success with the species.

METHODS

Ten adult *H. sorenseni* were collected at Santa Catalina Island and transported by ship to San Diego, February 18, 1971.[2] Four possessed gonads sufficiently mature to respond to spawning stimuli. Spawnings were induced on February 21 and 26 and March 1, using the thermal shock method (Ino, 1952), but in no case did fertilization occur in greater than about 5% of the eggs liberated. Observations of larval development and growth were carried out with progeny (approximately 1,000 trochophore larvae) obtained March 1 from a single male and female pair.

Fertilized eggs were 190 to 200 μ in diameter. Washing of eggs to remove excess sperm, mucus, and other possibly contaminating substances released during or prior to spawning was achieved by repeated suspension in filtered seawater (Millipore[3] filters, pore size 0.45 μ) following settling and decantation. After incubation of the eggs at 12 $\pm$ 2°C for 24-36 hr, larvae hatched at the trochophore stage. Because the swimming trochophores exhibited a strong negative geotaxis, they concentrated at the surface where they were easily drawn into a Pasteur pipette for transfer to experimental containers.

The effect of temperature on rate of development, settlement, and growth of recently settled juveniles was investigated using an aluminum thermal gradient block (Thomas, Scotten, and Bradshaw, 1963) with compartments bored to accommodate a series of 100-ml beakers. Each compartment could be illuminated from beneath to permit growth of algae within beakers. Containers, arranged in duplicate, were maintained at 10, 12, 14, 16, 18, and 20°C (each $\pm$ 0.5°C). The Pyrex beakers received 80 ml of Millipore-filtered and ultra-violet light treated seawater (Loosanoff and Davis, 1963). Twenty 72-hr veliger larvae were introduced into each together with 1 ml of a suspension of the food organism, *Nitzschia* sp., containing approximately 10,000 cells. To guard against salinity changes due to evaporation or condensation, each beaker was covered with a paraffin sheet, and the entire block insulated with foam styrene. Inspection was made on alternate days to determine the number of larvae surviving, settlement, and growth rate. The water was changed once weekly and new food supplied.

Approximately 500 larvae were distributed among five 1-liter Pyrex beakers at the time the thermal gradient erperiment was begun. These containers received a combination of about 10 species of pennate diatoms collected from illuminated aquarium surfaces in the laboratory (chiefly *Nitzschia*, *Grammatophora*, and *Navicula*). A thermal environment of 15-17°C was maintained.

DESCRIPTION OF LARVAE

The reader seeking details of morphogenesis in haliotids should refer to illustrations and text as provided for Japanese species by Ino (1952) and Ōba (1964), early development of which closely parallels American members of the genus. In this paper an effort is made to indicate distinctive features of *H. sorenseni* larvae.

Trochophores were subcylindrical in outline, bore a distinct prototroch and were yellow-tan in color. At 15-16°C, the roughly symmetrical shape of the trochophore was soon lost and by 48 hr after fertilization the early veliger form was attained with the incipient cap-shaped shell and lobular velum becoming defined. At 72 hr, the larval shell had taken the typical gastropodan snail-form complete with operculum while shell musculature, viscera, eye-spots, and velum were well developed. At the same time the foot and cephalic tentacles began to differentiate (Figure 1). Tissue pigmentation was predominantly beige, velar fringes were yellow, and the

[2] Collections were made at a depth of about 70 ft by T. Tutschulte and were timed to sample the peak of the reproductive season at the Isthmus station.

[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

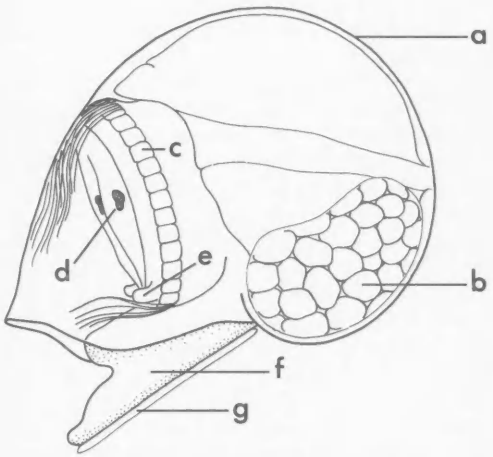

FIGURE 1.—Three-day veliger larva of *Haliotis sorenseni*. (Shell diameter, 270 μ) a. shell, b. digestive gland, c. velum, d. eye spot, e. incipient cephalic tentacle, f. foot, g. operculum.

digestive gland was maroon. Swimming of veligers at this stage carried them throughout the water column.

Settlement occurred at 9-10 days at 15°C. Velar dystrophy, with loss of ciliated fringes, took place gradually, and larvae retained the ability to swim if dislodged for several days after initial settlement.

INFLUENCE OF TEMPERATURE ON DEVELOPMENT RATE

Larvae confined to 100-ml beakers in the thermal gradient block appeared, except for the temperature effects to be described, to be normal in appearance and behavior and were similar to larvae maintained in liter beakers at 15-17°C. Development was most rapid at higher temperatures; some individuals settled as early as the 7th day at 20°C and the 8th day at 18°C. By the 15th day almost all larvae at the two highest temperatures had settled, yet none had settled at 10°C (Table 1, Figures 2 and 3). By the 25th day most larvae at 10°C had succumbed, having progressed only to the late veliger stage. Settling rate varied within groups, and even at 18°C approximately 5% did not settle.

Observations at the end of the 36-day experiment revealed that survival was best at 16° and 18°C, somewhat less at 20° and least at 14° and below. Larvae maintained at 10°C did not survive beyond 25 days and most of those at 12° failed at 25 to 30 days. Size attained by settled juveniles corresponded with survival; at 36 days shell lengths as great as 1.2 mm were attained at 18°C, about 1.0 mm at 20° and 16°C, and only 0.6 mm at 12° and 14°C.

GROWTH OF JUVENILE *H. SORENSENI*

Approximately 100 settled juveniles were obtained from the larvae reared in liter Pyrex beakers at 15-17°C. These individuals were carefully dislodged by a jetting stream of water and teasing needle and transferred to larger containers to observe growth and behavior under a variety of food and water flow situations. Food quality and quantity was not limited to insure maximum growth, hence a wide variety of food organisms was provided (pennate diatoms and filamentous red, green, and brown algae).

TABLE 1.—Number of *Haliotis sorenseni* larvae surviving and settled at 15 days in thermal gradient experiment.

Temperature	Series I			Series II		
	Surviving	Settled	Survivors settled	Surviving	Settled	Survivors settled
°C ± 0.5°	*No.*	*No.*	*%*	*No.*	*No.*	*%*
10	5	0	0	18	0	0
12	7	4	57.2	15	10	66.6
14	15	11	73.4	18	14	77.7
16	12	11	91.5	14	11	78.5
18	9	9	100.0	17	15	88.4
20	7	7	100.0	13	11	84.6

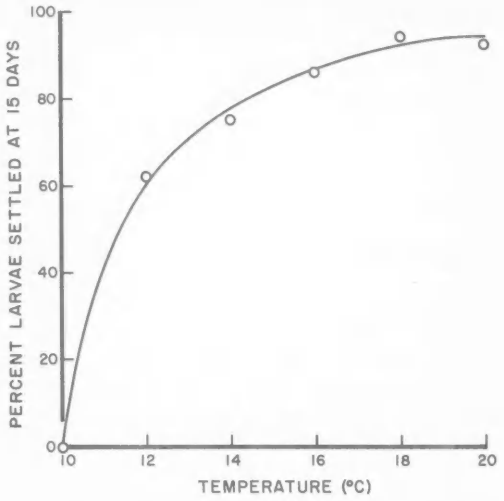

FIGURE 2.—Percentage of larvae firmly settled at 15 days. Points are averages for duplicate observations. Settlement was considered complete when larvae could no longer be dislodged by jetting a stream of water from a pipette.

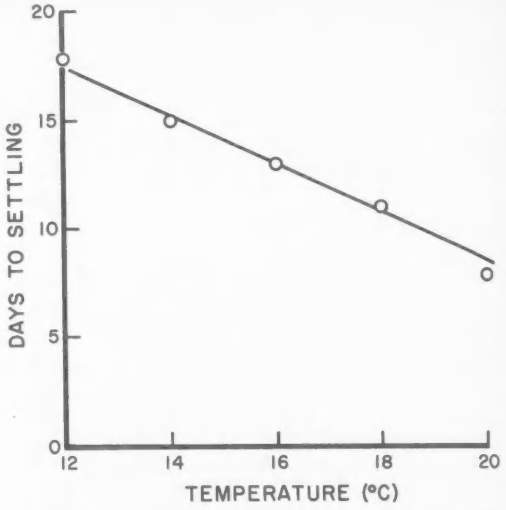

FIGURE 3.—Days to settlement of at least 75% of *Haliotis sorenseni* larvae from groups held at five different temperatures. Not more than 75% of the larvae at 12°C successfully settled, and none of those at 10°C reached this stage.

A marked variation in growth rate existed, even among those individuals which were provided surfaces (such as plastic and glass beakers) on which diatom growth appeared to be quite uniform. In one case, 19 individuals were retained in a liter beaker and provided mixed diatoms. At an age of 85 days some had attained a shell length of 4.5 mm while others were as small as 1.4 mm. The largest had formed four respiratory pores, yet the smallest was just beginning to form the first. Size attained at 100 days (15-19°C) ranged from 3.0 to 5.6 mm (mean, 4.25, SD $\pm$ 0.63 mm, $n = 19$). By 130 days the range was 4.0 to 8.0 (mean, 5.53 mm, SD $\pm$ 1.01 mm) in the same group (Figure 4).

DESCRIPTION OF JUVENILE SHELL FEATURES

The most conspicuous feature of recently settled and minute haliotids (less than 500 μ long) is the asymmetrical outline resulting from dextral growth of the persistomial shell. Through

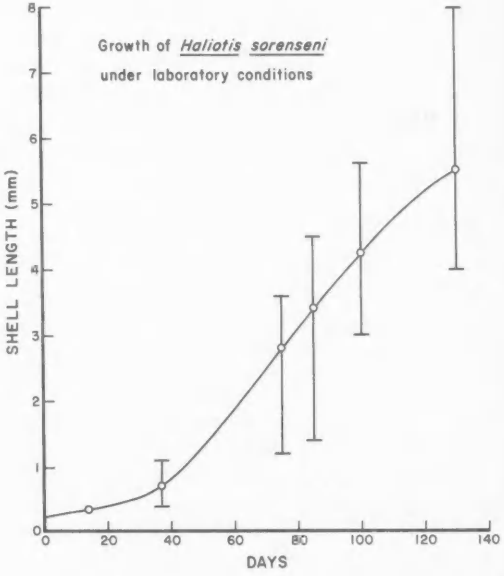

FIGURE 4.—Growth of larval and juvenile *Haliotis sorenseni* in 1-liter beakers provided mixed diatoms as food. Ranges of shell length are shown by vertical lines.

continued growth the asymmetry is reduced and the shell form, as viewed from above, is almost circular until the "notch stage" is reached. Formation of the first respiratory aperture is initiated by separation of two portions of the mantle at the right anterior margin interrupting otherwise uniform marginal shell deposition. The "notch" so formed is a convenient growth mark, reached by the most rapidly growing *H. sorenseni* at an age of 55 days and a shell length of 2.0 or 2.1 mm (Figure 5).

In the juvenile *H. sorenseni* observed, shell pigmentation was a pale violet-pink becoming more vivid as the notch stage was approached. In most cases a cyan-blue flare spread from the apex to the right shell margin. After completion of the first respiratory pore, a dichotomy in pigment pattern emerged. Although all juveniles developed from eggs of a single female, fertilized by a single male, approximately 40% developed an even red-violet shade throughout the greater extent of the shell while the majority became increasingly bicolored with growth. The bicolored pattern consisted of a rich red zone along the left edge of the shell (extending to the aperture row) and pigmentation of blue, green, and yellow over the broader surface right of the aperture row. In individuals of both coloration patterns, a conspicuous ivory-white patch remained at the position of attachment of the right shell muscle until obscured by nacre deposition at about 8 mm. The apex, in turn, became increasingly white.

Elevated apertures, typical of the species, appear even in first-pore individuals. More conspicuous is the ridge bordering the left shell margin. It is this ridge that forms the sharp corner and relatively straight left anterior margin (Figure 6).

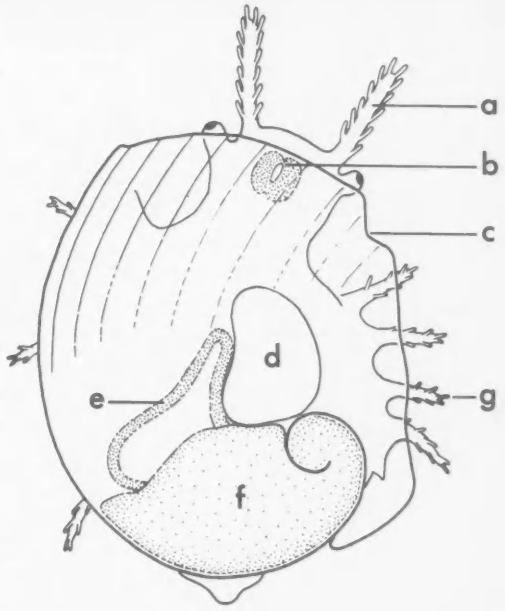

FIGURE 5.—Juvenile *Haliotis sorenseni* at "notch" stage (2.0 mm, 55 days). Shell is still slightly transparent and prominent anatomical features are readily seen from the dorsal aspect. a. cephalic tentacle, b. mouth, c. indentation at point of formation of first respiratory pore ("notch"), d. right shell muscle, e. intestine, f. digestive gland, g. epipodial tentacle.

DISCUSSION

Establishment of specific characteristics by which larvae and juveniles of the seven cooccurring California species of *Haliotis* may be distinguished must await results of studies of fine structure of larval shells. Examination by scanning electron microscope has revealed sufficient detail of fine crystalline and basement structure of larval shells in certain other prosobranchs (Fretter and Pilkington, 1971). Gross shell morphology alone is inadequate to differentiate larvae of even distantly related species. Pigmentation of velar and visceral portions may provide distinctive features for recognition of some species.

Pigments derived from parental yolk appear to be retained by trochophore and veliger larvae of *Haliotis*. Among California species, ovarian tissue is dark green in *H. rufescens, H. cracherodii, H. walallensis,* and *H. kamtschatkana assimilis*. Correspondingly, larvae of these species are conspicuously green. The remaining three species found locally, *H. fulgens, H. corrugata,* and *H. sorenseni,* produce eggs of brown, olive, and beige color, respectively. Their larvae

may be expected to reflect these pigments accordingly. I have examined larvae of *H. fulgens* which were generally brown but with green velar margins and those of *H. sorenseni*, which, as described above, were beige with yellowish velar margins. Tissues of larval *H. corrugata* are light yellow-green while velar fringes are a darker shade of green.

Color of the digestive gland in planktotrophic prosobranch larvae has been shown to reflect diet (Fretter and Montgomery, 1968). Since *Haliotis* veliger larvae are lecithotrophic, color of the digestive gland may have diagnostic value. The maroon-colored digestive gland of *H. sorenseni* veligers appears to be distinctive; I have not observed other than green or brown in the digestive glands of other haliotid veligers.

Although development of larvae and growth of settled juvenile *H. sorenseni* were more rapid at higher temperatures, survival was reduced at 20°C. More advanced juveniles, reared initially at 15-20°C, did not appear adversely affected by temperatures as high as 25°C. Possibly thermal tolerance limits are more restricted in larvae and recently settled individuals. Certainly other factors could have influenced success at higher temperatures. Despite weekly changes of water, bacterial, algal, and protozoan growth together with a build up of metabolites and reduced oxygen tensions in the relatively small volume of water used in the thermal gradient study could have influenced the results.

Larval *H. sorenseni* were not successful at 10-12°C. Water temperatures within the bathymetric range of the species may fall to 12° and occasionally to 11°C (e.g., at depths of 130 ft off Santa Catalina Island, T. Tutschulte, personal communication). Therefore the 10° or 12°C bathyisotherms may limit the depth to which larvae of *H. sorenseni* may successfully settle and grow. The results of the temperature block study indicate the range 14-18°C may be optimal for *H. sorenseni* larvae—an outcome not unexpected in view of the prevailing conditions in the natural environment from Pt. Conception to central Baja California.

Information on growth throughout the first days of life is available for several species of *Haliotis*. Ino (1952) reported that *H. discus* attained only 1.25-1.40 mm at 100 days and that the first respiratory pore was not formed until 130 days. In contrast, Ōba (1964) observed rapid early development of *H. diversicolor supertexta*. In that study, trochophores hatched at only 6 hr, veligers developed within 11 hr and settled by 2 days. The first respiratory pore was formed as soon as 23 days after fertilization. Interpolating from his growth curve, 100-day juveniles ranged from 8 to 13 mm (Ōba et al., 1968). In Ino's study, water temperatures declined from 18° to 10°C through the course of observations while Ōba's work was carried out during the summer and fall when temperatures ranged between 20° and 28°C. Whether the different development rates in these two species reflect specific contrasts or thermal influences is not clear. In another study (Kan-no and Kikuchi, 1962), *H. discus hannai* was reared at a relatively constant intermediate temperature (19-20°C). This species also exhibited rapid early development, settling in 3 days. Juveniles reached 11 mm in length at 100 days and 26 mm at 180 days.

The rather extreme variability in growth rate observed in *H. sorenseni* has also been found in *H. rufescens* (Leighton, unpublished data). Comparable variability is reflected in Ōba's growth curve for *H. diversicolor supertexta*. Differences in growth rate may reflect variation in food availability. In the present study, care was taken to provide uniform food distribution and feeding conditions. Yet within a single container, even within sampled subareas, a full spectrum of size variation could be found. The hypothesis may be advanced that gametogenic inequalities (e.g., yolk allotment) may be involved giving greater advantage to some individuals over others. Indeed, mortalities were more common among the smaller and presumably less active members.

Inherent variability in growth rate may be expected in nature to be complicated by differential quality and availability of food. Multimodal size-frequency distributions obtained for juvenile *Haliotis* populations in the field have been concluded to reflect multiple spawnings and recruitment waves (Leighton and Boolootian, 1963; Boolootian, Farmanfarmaian, and Giese,

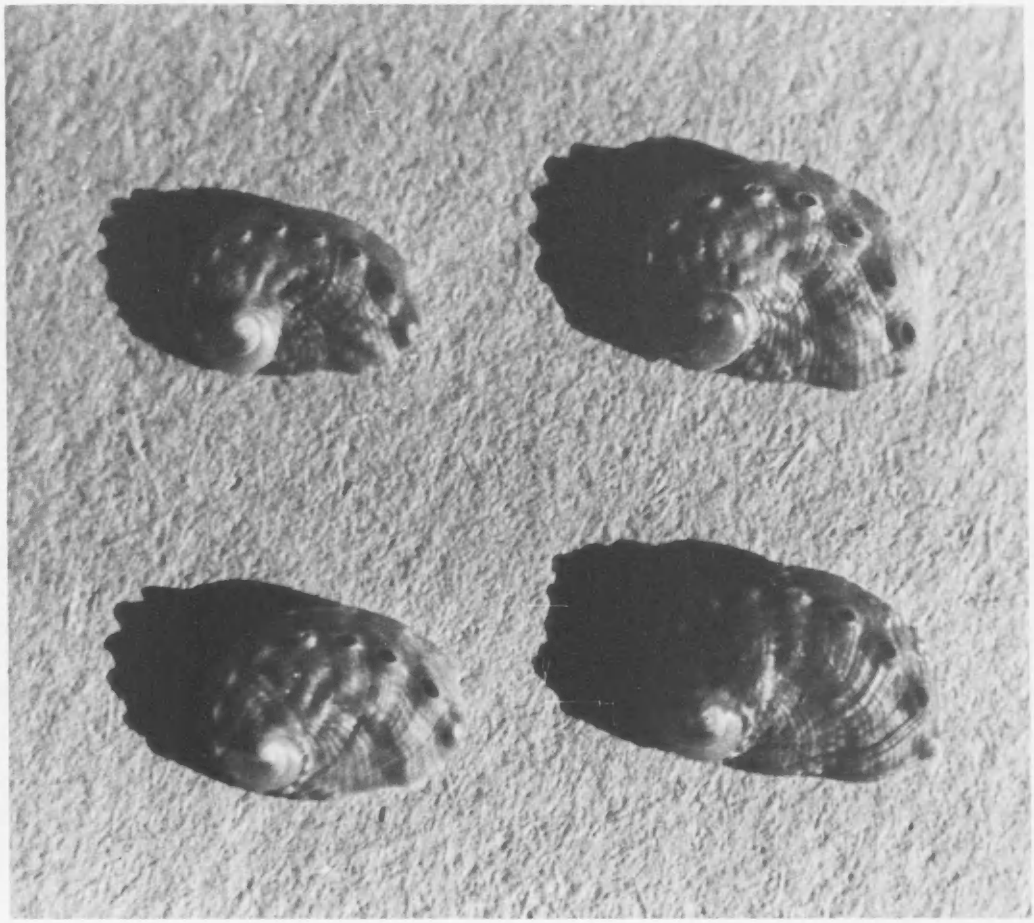

FIGURE 6.—Photograph of shells of juvenile *Haliotis sorenseni* representing the bicolored (above) and red pattern (below). Shells range in length from 6.6 to 8.4 mm.

1962). The evidence from this study suggests the assumption of uniform growth within a population of juvenile *Haliotis* is untenable and that conclusions regarding settlement date estimated from sizes of members of a sample must be drawn cautiously.

ACKNOWLEDGMENTS

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EXPLOITATION EFFECTS UPON INTERSPECIFIC RELATIONSHIPS IN MARINE ECOSYSTEMS[1]

SAUL B. SAILA AND JAMES D. PARRISH[2]

ABSTRACT

Due to man's continuing efforts to extract greater harvests of marine organisms from the world ocean, it is becoming increasingly important to be able to predict the consequences of exploitation on complex assemblages of organisms. These assemblages, or ecosystems, consist of predator and prey organisms in various interacting combinations. Preliminary evidence available from studies of marine invertebrate communities in coastal areas has indicated that removal of grazing herbivores or predators at various levels results in lower species diversity and greater instability of the ecosystem. In order to permit a quantitative evaluation of the effects of various rates and types of exploitation on interspecific relationships, model ecosystems were constructed utilizing a subset of graph theory as applied to network analysis. A basic ecological trophic unit was formulated, and these units were combined to form more complex model ecosystems. In particular, a hypothetical four species system of interacting predator and prey organisms was analyzed to demonstrate the consequences of varying certain model coefficients, especially rates of exploitation. It was shown that nonselective exploitation tended to maintain stability of the system better than highly selective exploitation. A hypothetical example of an empirical approach for examining changes in community structure was also demonstrated.

Much of the present theory of fisheries science as well as many practical fisheries management techniques are based on the concept of a single species or unit stock (Beverton and Holt, 1957; Ricker, 1958). This approach continues to be useful in describing and predicting the behavior of fisheries consisting primarily of a single species. Recently, Walters (1969) developed a deterministic computer simulation model for determining optimum harvest strategies based on a unit stock. However, modern fishing seems to be progressing toward exploitation on many species of the larger animals in aquatic ecosystems. To some extent this is due to the tendency toward reduction to meal of many species of fishes. Some obvious areas for the future development of marine fisheries will be in tropical or subtropical waters, such as parts of the Indian Ocean as well as the southeast and southwest Atlantic. These areas are characterized by a relatively greater diversity of species than the traditional fishing grounds of north-temperate regions. It can reasonably be expected that some species will be exploited intensively from them. It therefore seems desirable to attempt to better understand trophic relations of ecosystems consisting of several interacting species in order to develop management techniques for these systems. This increased understanding includes the effects of various kinds of exploitation strategies as well as environmental perturbations on these ecosystems. It is suggested that stresses applied to ecosystems may produce somewhat similar effects, regardless of their origin.

Some of the large volume of literature concerning diversity and stability in terrestrial as well as aquatic ecosystems has been reviewed at a recent symposium (Woodwell and Smith,

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1969). One of the generalizations which appeared to emerge from the symposium was that ecosystems characterized by high species diversity tended to be relatively stable. Elton (1958) has shown that if a predator has several alternate prey species to utilize, it will persist even if one of the prey becomes very scarce. Thus, it seems as if there is some correlation between diversity and stability.

In the case of marine invertebrates, there is some observational evidence (Paine, 1963) to indicate that marine predators at high levels in the food chain feed on more species of prey than do those on lower levels. Observations, such as the above mentioned, have led some ecologists to suggest that high level predators might contribute more to community stability than the lower level predators.

Removal of predators from rocky shore invertebrate communities (Paine, 1966) resulted in a reduction of the species diversity of the animal community. In addition, removal of grazing herbivores from rocky shores has resulted in the rapid growth of some of the formerly eaten plant species and a change in community composition toward lower species diversity (Jones, 1948; Southward, 1964; Paine and Vadas, 1969). The observations and experiments of Paine (1966) also indicated that diversity among competing species of marine invertebrates could be decreased by removal of predators in some instances. A theoretical dynamic analysis (Parrish and Saila, 1970) of a trophic subweb using Lotka-Volterra type interactions offered some support to Paine's conclusions.

With the exception of some pioneering conceptual work by Larkin (1963, 1966) in describing models for interspecific competition and exploitation applied to natural fisheries, very little seems to have been done in an effort to predict the effects of man's activities on aquatic communities consisting of several interacting species. One of the reasons for this appears to lie in the degree of complexity required to establish and express all the basic interrelationships in such a system (Mann, 1969). Recently, Menshutkin (1969) suggested graph theory as a useful tool for minimizing some of the difficulties of constructing models of interacting systems if certain simplifying assumptions, such as linearity and steady-state conditions, could be tolerated. Recognizing that any set of mathematical equations represents at best a crude approximation of the actual behavior of complex ecosystems and that empirical values of coefficients for complex models are largely unavailable, we have proceeded under the assumption that the simplest models should first be explored and carefully evaluated before proceeding to more elaborate formulations. In addition, it is believed that the simplicity of the methods described herein may enhance their utility, especially when considering the initial effects of exploitation or environmental modification on interacting ecosystems.

The objectives of this work were to: (a) introduce a subset of graph theory as used in network analysis; (b) describe a graph theoretic formulation of a basic ecological trophic unit, and to demonstrate some effects of predation and exploitation on model ecosystems consisting of these units; and (c) demonstrate some other uses of graph theory with a view toward stimulating further interest in its applications.

BACKGROUND AND DEVELOPMENT

By definition, a graph is a set of vertices (nodes) connected by a set of edges (branches). If the graph has polarity or direction, the edges have arrows, and the graph is said to be directed. In this report we are concerned only with directed graphs. Two very simple directed graphs are illustrated in Figure 1.

The ecological graphs utilized herein are based largely on graph theoretical techniques of network analysis, for which the theory has been clearly and concisely presented by Mason and Zimmermann (1960). To analyze a network, each edge connecting two vertices is given a coefficient, a "transfer function" or "branch transmission." The "transmission" from one vertex A to a distant one C can then be expressed as a combination of these individual coefficients. The important principle is that the value of any vertex is the sum of the directed inputs, regardless of the outputs. In the very simple case of Fig-

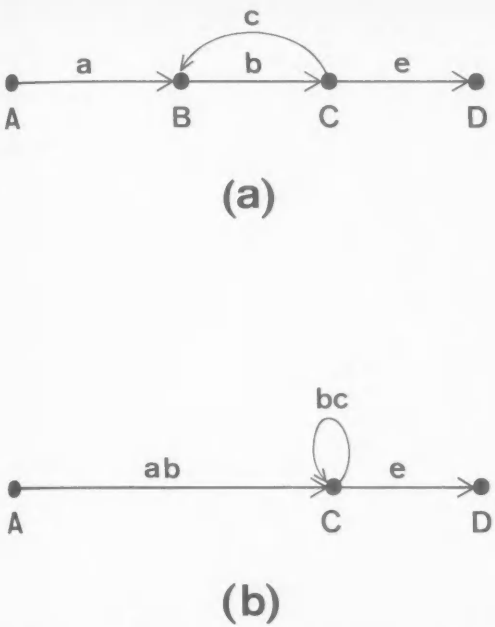


FIGURE 1.—An illustration of two simple directed graphs. A "self-loop" is shown in part (b) of the figure.

ure 1(a), the value of B is equal to the input from A plus the input from C:

$$B = aA + cC. \quad (1)$$

Similarly, the value of C is equal to the only input:

$$C = bB. \quad (2)$$

Substituting B from Equation (1) into Equation (2) and solving for C gives:

$$C = \frac{abA}{1-bc} . \quad (3)$$

Thus the ratio of the value of C to the value of A is:

$$\frac{C}{A} = \frac{ab}{1 - bc} , \quad (4)$$

which is the transmission from A to C. This type of term is used later as a biomass ratio or "trophic efficiency."

It can easily be seen that the graph in Figure 1 simply represents a set of linear algebraic equations. Such sets of equations can, of course, be solved classically. However, solution by inspection of some graphs or parts of graphs is possible. For example, in the graph of Figure 1(a), observe that:

$$C = (a \times b) \times A + (c \times b) \times C. \quad (5)$$

The graph can be simplified to that shown in Figure 1(b). A "self-loop" has been created that has the effect of making the value of C to be $\frac{1}{1 - \text{loop transmission coefficient}}$ times what it would have been without the loop. The situation becomes only slightly more complex when the transmission from A to D is considered. The value of D can be obtained from the value of C in Equation (3) as:

$$D = eC = e \cdot \frac{abA}{1 - bc} . \quad (6)$$

Or, making use of the known effect of a self-loop, it is possible to simply see by inspection of Figure 1(b) that:

$$D = (abe)A \cdot \frac{1}{1 - bc} = e \frac{abA}{1 - bc} \quad (7)$$

These simple principles and techniques are considered adequate for formulating some useful trophic graphs.

GRAPH OF A TROPHIC UNIT

Graph theory has been applied to the analysis of a variety of problems in engineering, operations research, and the social sciences (Berge, 1958; Busacker and Saaty, 1965; Kaufmann, 1967; Harary, 1969). Its use in biological sciences has been much more limited. However, Benzer (1959) and Maruyama and Yasuda (1970) have applied these concepts to genetics, and Landau (1955) and Trucco (1957) have used graph theory in describing animal behavioral problems. Menshutkin (1969) appears to have been the first to apply graph theory to the study of communities of aquatic organisms. He used graph theory to derive expressions to illustrate the relationship of the biomass of harvested organisms (fish) to primary production under

specific conditions. He graphed the relationship between a prey and a predator as shown in Figure 2(a). For simplicity, all the vertices (capital letters) can be standardized in energy units (or energy per unit time). The lower case coefficients are dimensionless constants or have a dimension of reciprocal time with values between zero and 1.0. Vertices and coefficients are listed in Table 1. Subscript 1 refers to the prey and subscript 2 refers to the predator. When another trophic level is added later, use of these subscripts can be easily extrapolated. For example, D_{12} in Figure 2(a) is the amount of Prey 1 accessible to Predator 2; D_{24} in a later graph is the amount of Prey 2 accessible to Predator 4.

The symbols used in Figure 2 are further defined in the following manner.

TABLE 1.—Description of the vertices and coefficients utilized in model development.

P	= (net) production	
Q	= loss by "respiration"	
q	= "respiration" coefficient	$Q = qB$
B	= biomass	
M	= loss by natural mortality	
m	= natural mortality coefficient	$M = mB$
F	= loss by exploitation (fishing)	
f	= exploitation coefficient	$F = fB$
U	= loss in undigested or unassimilated food	
R	= actual food ration	$U = (1 - k)R$
kR	= food assimilated (gross production)	
k	= digestion or assimilation coefficient	
P	$= kR - Q$	
D_{12}	= accessible food	
d_{12}	= accessibility coefficient	$D_{12} = d_{12}B_1$
H_{12}	= maximum ration (most a predator would ever consume)	
h_{12}	= maximum ration coefficient	$H_{12} = h_{12}B_2$
R_{12}	$= a_{12}H_{12} + b_{12}\delta_{12}$	
δ_{12}	$= D_{12} - H_{12}$	
a_{12}, b_{12}		feeding coefficient

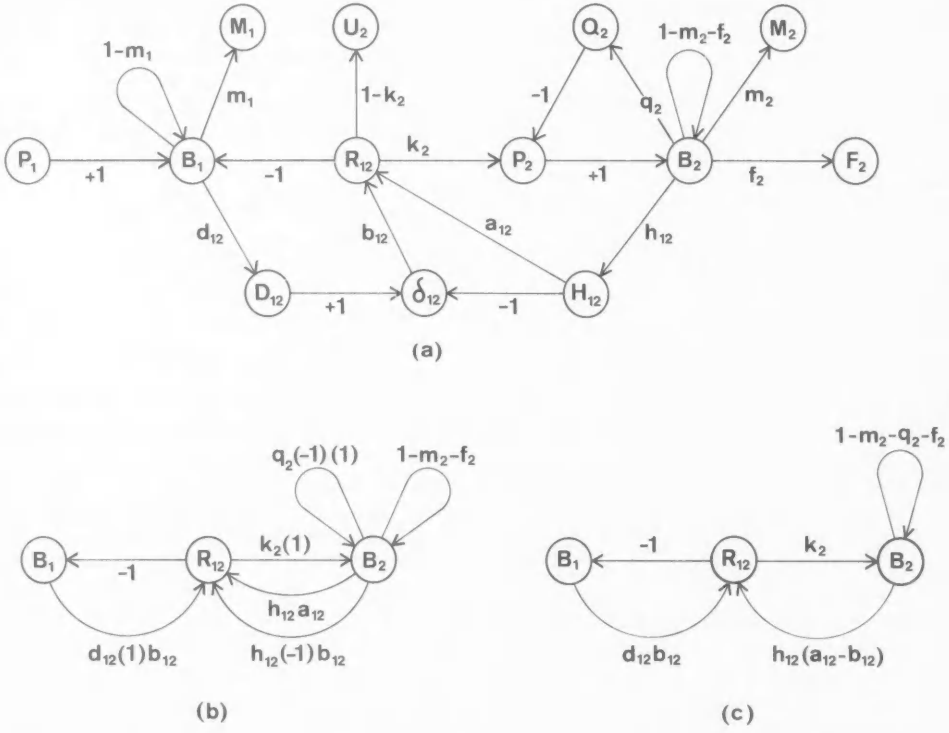


FIGURE 2.—Trophic graphs of Species 2 preying on Species 1. Part (a) illustrates Menshutkin's (1969) original formulation, and parts (b) and (c) represent the successive application of network analysis to obtain the basic trophic unit.

P in the graph is what is usually called net production (an energy rate). Net production P, is equal to gross production, i.e., assimilated food, kR, minus respiration, Q. Summing inputs at the graph vertex P_2, the value of P_2 is:

$$P_2 = k_2R_{12} - Q_2 . \qquad (8)$$

Respiration, Q, is expressed as the product of biomass and a "respiration coefficient," q:

$$Q = qB,$$

where B is the biomass (standing energy crop) of a species.

M is natural mortality, considered proportional to biomass;

$$M_1 = m_1B_1, \qquad M_2 = m_2B_2. \qquad (9)$$

Constancy of these coefficients is assumed.

F is fishing mortality which is used if an exploited population is considered. Death due to any other specific cause can be separately considered in a similar manner.

U is energy in the undigested (unassimilated) portion of food eaten, and k is the "digestion coefficient." The predator assimilates a fraction k of the ration R eaten, and the remaining energy, $U = (1 - k)R$, is lost.

Upon first inspection of the graph, it may be disconcerting to see vertices representing quantities such as biomass (energy) in the graph with vertices representing quantities such as production (energy per unit time). The confusion is resolved by realizing that the graph is not a pure flow network. It merely shows some assumed relationships, and at each vertex the same rules apply. For example, at vertex B_1 in Figure 2(a):

$$B_1 = (+1)P_1 + (-1)R_{12} + (1 - m_1)B_1, \qquad (10)$$

or,

$$P_1 - B_1 + B_1 - m_1B_1 = R_{12}. \qquad (11)$$

Net production — Natural mortality = Remainder eaten by predators.

Thus interpreted, the graph represents the relationships correctly.

An important feature of this formulation is the attempt to approximate the density dependence of feeding rate. Formulations for species interactions such as the classic equations of Lotka and Volterra express rates of change of the number or biomass of a species as products of coefficients and numbers or biomass of the interacting species. This approach has involved the assumption that feeding rate is independent of the abundance of prey and it is an oversimplification which results in an inherently unstable system. The experimental work of Ivlev (1961) provided a density-dependent feeding relation:

$$R = H\,(1 - e^{-\eta p}), \qquad (12)$$

where: H = the "maximum ration" of the predator, the most it would ever eat (or the maximum rate at which it would feed) no matter how much food were available;
R = the "actual ration" of the predator, the amount actually eaten (or the rate at which it feeds) under an actual condition of food availability;
p = the density or biomass of the prey population;
and η = a coefficient.

A linear approximation of this relationship, following Menshutkin (1969), can be used in the graph model. A parameter δ_{12} is defined as:

$$\delta_{12} = D_{12} - H_{12} , \qquad (13)$$

where: D_{12} = the amount of the prey biomass accessible to the predator $D_{12} = d_{12}B_1$. A constant of proportionality to prey biomass is assumed.
H_{12} = as defined above. Since H_{12} is obtained as a fraction of predator biomass ($H_{12} = h_{12}B_2$), the assumption is introduced that all predator individuals feed at the same rate.

The "actual ration" of the predator is then defined as:

$$R_{12} = a_{12}H_{12} + b_{12}\delta_{12} , \qquad (14)$$

where a_{12} and b_{12} are fractional coefficients.

This linear expression is used to approximate the following modification of Ivlev's exponential relation:

$$R = H(1 - e^{-\xi \frac{D}{H}}), \qquad (15)$$

where D and H are defined as before.

The implementation of Equation (14) in the graph of Figure 2(a) is seen by summing inputs at vertex δ_{12}:

$$\delta_{12} = (+1)D_{12} + (-1)H_{12} = D_{12} - H_{12}, \qquad (16)$$

and at vertex R_{12}:

$$R_{12} = a_{12}H_{12} + b_{12}\delta_{12}. \qquad (17)$$

Although lacking in mathematical rigor, this linear approximation can be made to give reasonably accurate results over a limited range of prey density, and it is considered to be an improvement over the simple density-independent assumption. Figure 3 provides a sample comparison of an Ivlev exponential relationship according to Equation (15) with the linear approximation of Equation (14). The coefficients a and b should, of course, be chosen in any real case to approximate either a desired analytic function of known utility or a set of data on feeding observations.

The "network analysis" techniques described previously were applied to the graph of Figure 2(a) to produce the simplified graphs shown as Figure 2(b) and Figure 2(c). The derivations

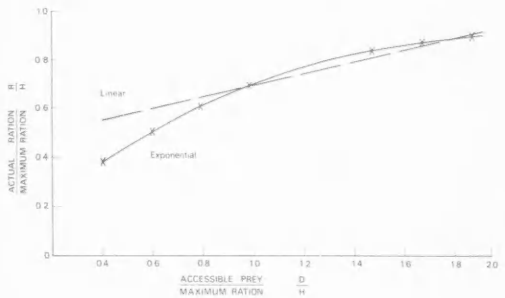


FIGURE 3.—Linear and exponential approximations of feeding behavior.

used do not require P_1 or m_1. Furthermore, M_1, M_2, and U_2 cannot give "inputs" at any vertex since they are all directed outward. Therefore, the above parameters were eliminated with no effect on the solutions. Vertices P_2 and Q_2 were absorbed using graph theory network techniques to produce Figure 2(b). The same figure shows the similar absorption of vertices D_{12}, δ_{12}, and H_{12}. Parallel inputs to a vertex can be combined. In this case, the two self-loops at vertex B_2 were combined, and the two edges from B_2 to R_{12} were combined. The resulting simplified graph, Figure 2(c), is the most basic graph that expresses the assumed relationships.

The above formulation describes a two-species predation model where Species 2 preys on Species 1. At this trophic level, and for the formulations to be used, the term "predation" is applied in its broadest sense. Since the formulation does not make use of production, mortality or any other vital property of Species 1, Species 1 is really just a resource. It could be vegetation, or with some reinterpretation of coefficients, even living space. Clearly, the above graph is a building block from which a variety of more complex food webs can be constructed. Only limited applications of this concept are made in the following material, and its validity awaits the test of further applications.

SOME MODELS AND THEIR INTERPRETATION

Since relatively little observational information is available concerning the important problem of community interactions, it was believed that a model study such as this might assist in a further understanding when additional observational data are taken.

Competitive and predatory interactions, with and without exploitation, were examined using trophic graphs made from the building block developed previously. Figure 4 shows Species 2 and Species 3 competing in their utilization of resource B_1. A relation was derived for the ratio of the biomass of each of the competitors to that of the resource: B_2/B_1 and B_3/B_1. In either case this was done by writing the very simple linear equations for each of two vertices

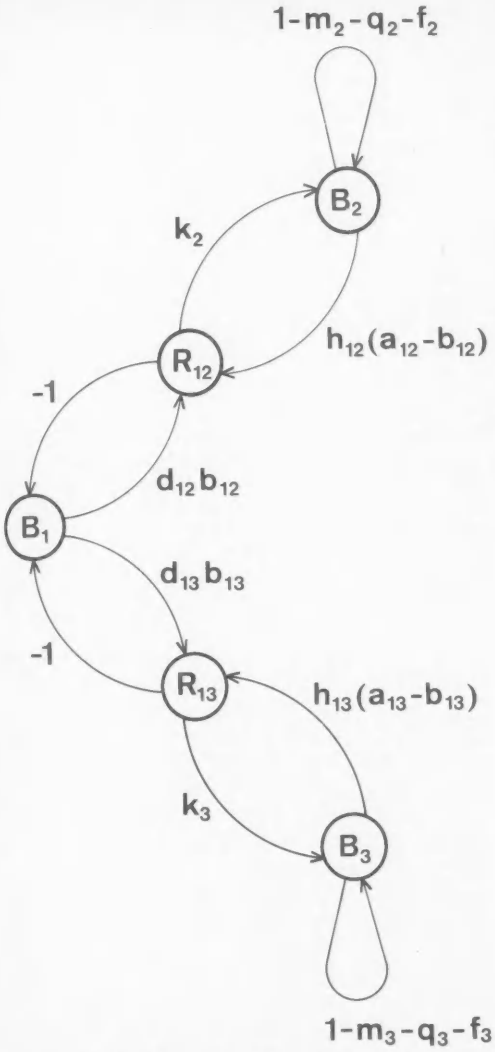


FIGURE 4.—Trophic graph of Species 2 and Species 3 preying on Species 1.

and solving them simultaneously in the classical manner. For competitor Species 2, R_{12} was written as the sum of its inputs in the graph, and B_2 was written as the sum of its own inputs. In this case there are two equations in the three variables B_2, B_1, and R_{12}. R_{12} was eliminated to give B_2/B_1 in terms of coefficients. B_3/B_1 was derived in a similar manner, and division gave the ratio of the biomass of the two competing species B_2/B_3 as follows:

$$\frac{B_2}{B_3} = \frac{k_2 d_{12} b_{12} V}{k_3 d_{13} b_{13} V'} \qquad (18)$$

where: $V = m_3 + q_3 + f_3 - k_3 h_{13}(a_{13} - b_{13})$

$V' = m_2 + q_2 + f_2 - k_2 h_{12}(a_{12} - b_{12})$

Inspection of Equation (18) reveals that if the two species compete exactly equally, or are exploited equally, the ratio is unity. This is entirely the expected result. By giving one species or the other a competitive edge in one or another of the coefficients, it is apparent that the B_2/B_3 ratio can be changed.

The simplest subweb involving predation on two competing species is shown in Figure 5. In this subweb Species 4 preys on Species 2 and Species 3, and Species 2 and Species 3 prey on Species 1. The procedure for deriving the ratios B_2/B_1 and B_3/B_1 was exactly as described above. That is, an equation was written for each

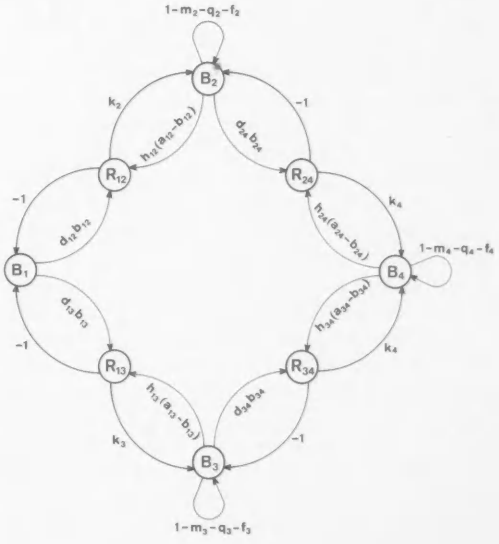


FIGURE 5.—Trophic graph of a 4-species subweb. In this case Species 4 preys on Species 2 and Species 3, and Species 2 and Species 3 prey on Species 1.

vertex except B_1, and the equations were solved simultaneously. In this case there are seven equations, and the work of classical solution was not excessive. The result was found to be:

$$\frac{B_2}{B_3} = \frac{W - k_2 d_{12} b_{12}(XY + Z)}{W' - k_3 d_{13} b_{13}(XY' + Z')} \quad (19)$$

where:

$$\begin{aligned}
W &= k_3 k_4 d_{13} b_{13} d_{34} b_{34} h_{24}(a_{24} - b_{24}) \\
W' &= k_2 k_4 d_{12} b_{12} d_{24} b_{24} h_{34}(a_{34} - b_{34}) \\
X &= k_4 h_{24}(a_{24} - b_{24}) + k_4 h_{34}(a_{34} - b_{34}) \\
&\quad - m_4 - q_4 - f_4 \\
Y &= k_3 h_{13}(a_{13} - b_{13}) - d_{34} b_{34} - m_3 - q_3 - f_3 \\
Y' &= k_2 h_{12}(a_{12} - b_{12}) - d_{24} b_{24} - m_2 - q_2 - f_2 \\
Z &= k_4 d_{34} b_{34} h_{34}(a_{34} - b_{34}) \\
Z' &= k_4 d_{24} b_{24} h_{24}(a_{24} - b_{24})
\end{aligned}$$

Questions of interest here were the effects on biomass ratios of the competitors as a function of various competitive coefficients and exploitation, and the difference in these effects with and without predation on the competitors. "Coefficient" values from Menshutkin (1969) were introduced for the coefficients for predation by Species 4 on Species 2 and Species 3 (the same coefficients for both—equal predation). Basically the same coefficients were used for the competition of Species 2 and Species 3 as well. Coefficients were held constant except for the one whose effect was being considered. Using such values, the equations were simplified, and in most cases Species 3 was then given the nominal value of the competitive variable of interest while the value of that variable for Species 2 was made to vary above and below the nominal. This range of variation of Species 2 was expressed as the ratio coefficient 2/coefficient 3. The same process was performed for the earlier formulation without predation (Equation 18). Thus ratios B_2/B_3 were obtained from both cases—with and without predation.

A brief examination was made of the effect of various exploitation strategies on the relative stability of two model ecosystems, one with predation and one without predation. These systems are described by Equations (18) and (19), and stability was measured by the change in biomass. Figure 6 illustrates the results of various types of exploitation on the two systems. It is

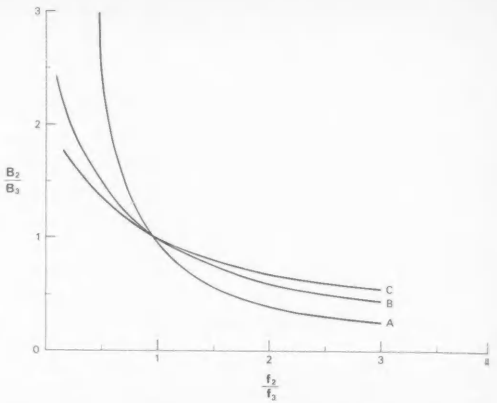


FIGURE 6.—Effects of predation and exploitation on model ecosystem stability as measured by biomass ratios. Curve A illustrates a 4-species subweb in which there is no exploitation of the top predator. Curve B illustrates a 3-species subweb with no top predator. Curve C illustrates a 4-species subweb with exploitation of the top predator as well as prey species 2 and 3. All numerical values of coefficients are from Menshutkin (1969). The nominal value of f_3 was taken as 0.3.

apparent from an examination of this figure that the most stable conditions examined involved predation as well as exploitation of the predator and the prey species. However, the system involving no top predator seemed to be more stable under exploitation of both prey species than the system involving predation, but with no exploitation of the top predator.

For different types of competitive advantage of one species over the other, the effect of predation on biomass ratios may be very different. Figure 7 demonstrates the effect of unequal competition in the coefficient d, which relates to the availability of the resource to Species 2 and Species 3. Without predation, the ratio B_2/B_3 of biomasses of the competitors is always the same as their d ratio. With predation, the ratio takes the much different form indicated. The values used for the d_{12}/d_{13} ratio ranged from 2.7 to 0.37. This range of values produces a full range of B_2/B_3 ratios, from the point where Species 3 becomes extinct, to the point where Species 2 becomes extinct. For the coefficient d, the results are not dependent upon the absolute value of d.

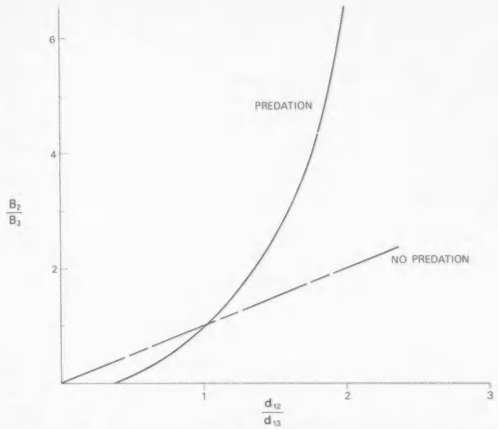
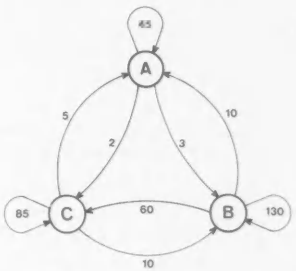


FIGURE 7.—An illustration of the effect of predation (as measured by biomass ratios) on competition as measured by changes in the ratio of the resource accessibility coefficient d for the two species.

The results shown in Figure 7 clearly indicate that some of the competitive coefficients have a very large influence on the relative stability of interacting systems. They suggest that if the stress of exploitation or other environmental stresses interact with other model coefficients as, for example, in a simple predator-prey interaction, the system may respond very violently, with the rapid extinction of one or the other of the competing species.

In some instances it may be desirable to have some rough empirical measure of the stability of exploited ecosystems consisting of interacting species. As Margalef (1969) has indicated, an adequate measure of community stability must include a measure of diversity as well as a measure of persistence. Furthermore, Margalef attempted to formulate a generalized mathematical model for their interdependence. It is suggested that an additional application of graph theory may also be utilized to provide some empirical indication of stability and persistence of communities subjected to either environmental or exploitive stresses, assuming certain types of background information are available.

Consider the following hypothetical example. Three communities of fishes (A, B, C) are subjected to various levels of exploitation. Assume that some crude index of diversity or community structure has been established which permits identification of the three communities as mutually exclusive groups. Assume that the three communities are sampled again during the course of a year, and that the frequency of samples which resemble the previously defined community as well as the frequency of samples which resemble the other two communities are listed. These frequencies can be displayed in the form of a network as shown in Figure 8. The data



$$F_0 = \begin{bmatrix} 45 & 3 & 2 & 50 \\ 10 & 130 & 60 & 200 \\ 5 & 10 & 85 & 100 \end{bmatrix} \qquad M = \begin{bmatrix} .90 & .06 & .04 \\ .05 & .65 & .30 \\ .05 & .10 & .85 \end{bmatrix}$$

$$M^2 = \begin{bmatrix} .8150 & .0970 & .0880 \\ .0925 & .4555 & .4520 \\ .0925 & .1530 & .7545 \end{bmatrix} \qquad P_0 = \begin{bmatrix} 50 & 200 & 100 \end{bmatrix}$$

$$P_0 M^2 = \begin{bmatrix} 50 & 200 & 100 \end{bmatrix} \begin{bmatrix} .8150 & .0970 & .0880 \\ .0925 & .4555 & .4520 \\ .0925 & .1530 & .7545 \end{bmatrix} = \begin{bmatrix} 68.50 & 111.25 & 170.25 \end{bmatrix}$$

FIGURE 8.—Example of a hypothetical network showing the frequencies of samples resembling their initial structure as well as those of the other two community structures. In this example F_0 is the matrix of frequencies at the end of the first sampling period, M is the corresponding probability matrix, M^2 is the square of the probability matrix and P_0 is the vector of frequencies by community type. P_0M^2 is the matrix-vector product expressing the expected new frequencies by community type at the end of the second sampling period under the assumption that the probability matrix remains constant during the time interval.

from the network is presented as a matrix (F_o of Figure 8) of frequencies which was normalized to form a probability matrix (M of Figure 8). This probability matrix M is one in which the i, j entry gives the proportion of the samples from community v_i which resembled community v_j during the sampling period. An important theorem concerning probability matrices states that if B and C are probability matrices, so is their product BC. A corollary to this theorem states that if M is a probability matrix, then so is every power M^n, for any positive integer n. If the assumption is made that the probability matrix M remains constant over time, then if one knows the initial frequency matrix F_o and the probability matrix M, it is possible to find the sample frequency distribution at a subsequent time t_n by finding the nth power of M and then forming the product P_oM^n where P_o is the vector of row sums equal to the initial vector of frequencies by community type. In our case the frequency in year 2 is $F_2 = P_oM^2$. This matrix-vector multiplication is illustrated in the lower part of Figure 8. It is suggested that this derived frequency might be useful as the expected value basis for comparison with the sample observations made during subsequent years, if it is assumed the probability matrix remains constant over time.

CONCLUSIONS

The examples provided in this study are given primarily to illustrate the wide range of possibilities for the use of graph theory in studying the stability of interacting competitive and predatory relationships. The tentative results of this model study suggest that a nonselective exploitation strategy, which includes both predator and prey organisms, may be "best" from the point of view of maintaining community stability in complex ecosystems. The high desirability of obtaining experimental values for certain coefficients was also pointed out.

The limitations of a linear, steady-state model are many and obvious. However, if such a model can sometimes be utilized to provide approximate results suitable for use in practical management at the early stages of marine ecosystem management, then the model is a worthwhile tool, and the method utilized has some merit. If the method (graph theory) can be used not only to obtain some basic insight into system behavior but can also be used as an empirical tool, then it seems particularly worthwhile. Both these possibilities seem to await the results of future imaginative development.

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NITROGEN EXCRETION BY ANCHOVY (*ENGRAULIS MORDAX* AND *E. RINGENS*) AND JACK MACKEREL (*TRACHURUS SYMMETRICUS*)[1]

JAMES J. MCCARTHY[2] AND TERRY E. WHITLEDGE[3]

ABSTRACT

Teleost fish have been shown to excrete a variety of nitrogenous substances among which are ammonia, urea, and creatine. Previous reports show values for excretion of nearshore or bottom fish but not of pelagic species.

Two species of anchovy and jack mackerel were placed in chambers and their nitrogenous excretion products were measured. Ammonia, urea, and creatine accounted for 82% of the total nitrogen excreted by *Engraulis mordax* and the identified fraction was 83% ammonia, 16% urea, and 1% creatine.

The significance of pelagic fish as a source of ammonia and urea in California coastal waters is discussed.

On the basis of the major end product of their protein catabolism, animals are classified as ammonotelic, ureotelic, and uricotelic. Although these categories can be useful in evolutionary considerations (Baldwin, 1964), they are somewhat arbitrary in that the excreta of most animals contain a mixture of ammonia, urea, and uric acid. Mammals, elasmobranch fish, some amphibians, and some reptiles are considered to be ureotelic; teleost fish, some amphibians, and most invertebrates are ammonotelic; and birds and some reptiles are uricotelic (Baldwin, 1964). In ureotelic animals urea is produced via the ornithine cycle. It is, however, unlikely that this metabolic pathway is operative in nonureotelic organisms such as some teleosts, which excrete substantial quantities of urea. Brown and Cohen (1960) have shown that no marine teleost has the enzymes necessary for the first two steps in the ornithine cycle. The complete complement of ornithine enzymes has been found in the coelacanth however (Brown and Brown, 1967).

Arginase is present in the livers of teleost fish and hence dietary arginine has been suggested as a source of urea (Hunter and Dauphinee, 1924-1925; Hunter, 1929), but this suggestion is considered unlikely since arginine is an essential amino acid for this group of organisms (Forster and Goldstein, 1969). Purine catabolism also has been suggested as a means of urea formation via uricolysis (Brunel, 1937), and in support of this Goldstein and Forster (1965) found uricolytic activity in the livers of five species of marine and freshwater teleosts.

Delaunay (1929), Grafflin and Gould (1936), Grollman (1929), and Smith (1929) determined the composition of the urine of eight species of marine teleosts and their results were summarized by Scheer and Ramimurthi (1968). The proportions of various components of the total nonprotein urinary nitrogen varied greatly within, as well as between, species (ammonia varied from 0.5 to 9.6%, urea varied from 0.1 to 30.8%, creatine varied from 6.5 to 61.7%, and amino-N varied from 4.0 to 21.4%). In 1929 Smith used a divided chamber to permit separate determinations of the nitrogen released by the gills and by the kidneys, and his results showed that essentially all of the ammonia and urea released originated from the gills. In addition to these compounds, the branchial excreta consisted of amine or amine oxide derivatives while the less diffusible nitrogenous end products such as creatine, creatinine, and uric acid were excreted solely by the kidneys. It is therefore

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apparent that a release rate with ecological significance would have to consider both branchial and renal release.

Since the only data available from which one can calculate nitrogenous release rates for marine teleosts are for nearshore or bottom fish such as the sculpin, the starry flounder, and the blue sea perch (Wood, 1958), the following work was undertaken using significant pelagic species in order to assess the importance of marine teleosts as a source of ammonia, urea, and creatine in the euphotic zone.

METHODS

Experiments with the northern anchovy, *Engraulis mordax*, were conducted in August 1970, in the laboratories of the Fshery-Oceanography Center, La Jolla, California. Between experiments the fish were kept in a tank of flowing seawater and, unless specified otherwise, were fed frozen brine shrimp daily. For each experiment ten fish were placed in a 32-liter circular Plexiglas chamber similar to that described by Lasker (1970). During the first experiment the chamber was darkened and 24°C seawater flowed through it at a constant and determined rate. Beginning at the time the fish were introduced, effluent was sampled at 10-min intervals for 40 min. The fish had not been fed for 24 hr. For experiments 2 and 3 the flowing system was not used. The chamber was filled initially with seawater and during the experiments was exposed to room light. The temperature during experiment 2 was 24°C and water samples were taken at 10-min intervals for 40 min. The fish had been fed 30 min prior to their placement in the chamber. The temperature during experiment 3 was 21.5°C and water samples were taken at 10-min intervals for 70 min. The fish had not been fed for 48 hr and just after the 30-min sampling, 2.49 g of frozen brine shrimp were thawed and added to the chamber (the first and second portions of experiment 3 will be referred to as 3a and 3b). An appropriate control was run to determine the effect of the brine shrimp on the ammonia, urea, creatine, and total nitrogen concentrations.

Ten fish from the group used for experiments 1 and 2 and the ten used for experiment 3 were sacrificed for weight determinations. Wet weight determinations were made after blotting the specimens on filter paper, and dry weight was determined after they had been dried at 60°C for 96 hr.

Experiments with the Peruvian anchovy, *Engraulis ringens*, were conducted off the coast of Peru in April 1969, during the RV *Thompson* cruise 36. The methods of collection were described by Whitledge and Packard (1971). Release rates for urea and ammonia were determined for each of three fish in separate one-liter volumes of 0.45μ m Millipore^R filtered seawater at 15°C. Each experiment was run until the animal died (approximately 90 min).

Experiments with the jack mackerel, *Trachurus symmetricus*, were conducted off the coast of California in July 1970, during a cruise of the RV *Alpha Helix* for the Institute of Marine Resources Food Chain Research Group. Of three specimens caught with lure and line, two were placed in a 42-liter Plexiglas deck tank which was continually flushed with surface seawater, and the third, which had been injured when caught, was sacrificed for a weight determination. After approximately 5 hr the fish were transferred to a similar tank recently cleaned and filled with 19°C surface seawater which had been filtered through a 173 μm nylon mesh. Samples for ammonia and urea analyses were taken at the beginning and at the conclusion of the experiment 2 hr later. The fish were kept another 20 hr and released.

For samples from the *E. ringens* experiments ammonia was determined by a modified form of Johnston's (1966) rubazoic acid method and urea by a urease hydrolysis coupled with the rubazoic acid method. In all other experiments ammonia was determined by the phenolhypochlorite method (Solórzano, 1969) and urea by the urease method (McCarthy, 1970). All determinations were made in duplicate immediately after each experiment. Creatine concentrations were measured using a fluorescent complex with alkaline ninhydrin (Whitledge and Dugdale, in press). Total nitrogen was determined with the ultraviolet oxidation technique

of Armstrong, Williams, and Strickland (1966) as described by Strickland and Parsons (1968), but modified by the addition of sodium hypochlorite (chlorine bleach, 5.25% active ingredients). One ml sodium hypochlorite per 100 ml sample was found to increase the percentage of conversion of creatine to nitrate. If added in excess, the sodium hypochlorite will react with the hydrogen peroxide to release oxygen. The conversion of a standard solution of creatine to nitrate in the digester was 43.4%, but the addition of sodium hypochlorite increased this value to 95.0%. Urea standards showed 96-100% conversion without addition of sodium hypochlorite.

All chambers were washed with either fresh or distilled water immediately prior to each experiment and experimental periods were kept to a minimum in an effort to reduce possible effects of bacteria. Antibiotics interfere with both of the ammonia methods mentioned above, and could not be used to reduce bacterial activity. Wood (1958) showed that in fish excretion experiments running as long as 24 hr, bacteria on the surface of the fish do not affect the results and the concentrations of released nitrogen compounds were unchanged for an additional 24 hr.

The data were analyzed statistically using the Mann Whitney U and the Tukey-Siegel tests to compare the medians and variabilities respectively. Significant differences between experiments were at the 0.05 level.

RESULTS

The release rates for ammonia, urea, creatine, total nitrogen and the ammonia-urea ratios for all experiments are given in Table 1. The results of the *E. mordax* experiments represent the mean of the 10-min interval samples for each experiment. An example of the data obtained in one of these experiments is shown in Figure 1. At the conclusion of the first *E. mordax* experiment all of the fish had acquired darkened dorsal coloration and one was locked into the panic response described below for *E. ringens*. Immediately after release into the large holding tank, food was added and all except the one panicked fish, which died a few hours later, fed normally and regained normal coloration. During the other experiments with *E. mordax*, the fish behaved normally and retained their normal coloration. The fish in the *E. mordax* experiment 3b were restricted from feeding in their normal frenzied manner because of the size of the chamber and at the conclusion a small portion of the food remained uneaten. Creatine and total nitrogen values for the second *E. mordax* experiment indicate that

TABLE 1.—Excretion of nitrogenous compounds by *Engraulis mordax*, *E. ringens*, and *Trachurus symmetricus*.

Species		μg at N/mg dry wt/day				
		Ammonia	Urea	Creatine	Total nitrogen	Ammonia-N / Urea-N
Engraulis mordax						
starved one day	(1)	0.074	0.020			3.70
fed before experiment	(2)	0.185	0.036	0.003	0.273	5.14
starved 2 days	(3a)	0.055	0.021	0.002		2.62
feeding	(3b)	0.076	0.023	0.003		3.45
Engraulis ringens	(1)	0.240	0.083	0.118	0.507	2.90
	(2)	0.281	0.089	0.111	0.700	3.16
	(3)	0.171	0.057	0.104	0.346	3.00
Trachurus symmetricus		0.090	0.017			5.29

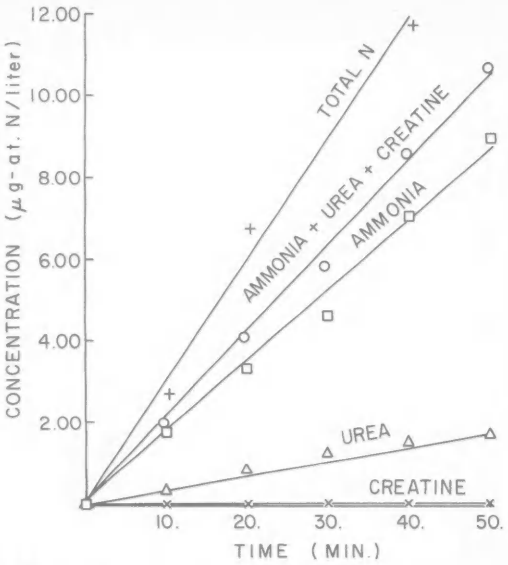

FIGURE 1.—Nitrogen excretion by 10 specimens of *Engraulis mordax* in experiment 2. Specimens were fed 30 min before experiment.

ammonia, urea, and creatine accounted for approximately 82.7, 16.0, and 1.3%, respectively, of the sum of the ammonia, urea, and creatine values. This sum was approximately 82% of the total nitrogen released. The fish used in the *E. mordax* experiments 1 and 2 had a mean wet weight of 13.9 g and a mean dry weight of 3.9 g per animal; those used in the third experiment had mean wet and dry weights, respectivly, of 15.2 g and 4.3 g per animal.

In the *E. ringens* experiments, the sum of the individually measured nitrogen compounds accounted for 69 to 96% of total nitrogen excreted. Relative amounts of ammonia, urea, and creatine averaged 44.6, 14.5, and 21.4%, respectively, while 19.5% was unidentified. Although the specimens of *E. ringens* appeared in good health for the first few hours after capture, their condition deteriorated rapidly after the experiment began. One lived for 83 min, another for 85 min, and the third for 105 min. The behavior pattern was a panic response in which the animals tried repeatedly to swim downward into the bottom of the container and eventually did considerable damage to their heads, resulting in broken blood vessels in their eyes and nasal regions. The dorsal coloration changed from a greenish-grey to jet black during the deterioration, and once an animal locked into this behavior pattern there was apparently no way to reverse it and death was inevitable. The mean wet weight and dry weight per fish for these experiments was 7.0 and 1.9 g, respectively, and nitrogen was found to be 10.9% of dry weight.

The results for the *T. symmetricus* represent a single value for both fish in the same chamber. Prior to, during, and in the 20 hr after the experiment the fish swam about the chamber in a calm manner. The wet weight of the sacrificed fish was 190.0 g.

DISCUSSION

The fish in the *E. mordax* experiment 2 were the most recently fed, and Figure 1 shows that urea, ammonia, and creatine were released at approximately constant rates over the experimental period. Table 1 shows that these release rates for ammonia, urea, and the ammonia-urea ratio were the highest of all the *E. mordax* experiments. The urea release rates for the other experiments (1, 3a, and 3b) were all similar, but the ammonia release rates and the ammonia-urea ratios appear to be related to the length of the starvation period.

For the *E. mordax* experiments, the statistical tests indicated that the ammonia release rates in experiments 1 and 3a and in experiments 1 and 3b were not significantly different within each pair with respect to central tendency. On the other hand there were significant differences between the pairs of ammonia release rates in experiments 1 and 2, 2 and 3a, and 2 and 3b. The variabilities for ammonia release rates for all of the experiments were similar. With regard to the urea release rates, only those for experiments 1 and 2 were significantly different with respect to location of central tendency and none of the experiments differed from each other with respect to variability.

These statistics imply that the effect of feeding is rapidly apparent in the ammonia release rates while it appears more slowly and to a lesser de-

gree in the urea release rates; this is clearly reflected in the ammonia-urea ratios. When the period of starvation was the greatest (experiment 3a) the ratio was the lowest, and when the starvation was least the ratio was the greatest. The ratio for experiment 3b presumably would have increased to a value comparable to that for experiment 2 when the time since feeding had become equal for both.

Upon thawing, the brine shrimp which were used to feed *E. mordax* liberated ammonia, urea, and creatine. If these substances were retained in large quantities by the shrimp, the results of experiments 2 and 3b could have been affected. Such interference is, however, unlikely since only the ammonia release rate increased with feeding in experiment 3. If this increased rate of release had resulted from ammonia liberated from the shrimp after ingestion by the fish, a comparable increase in the rate of urea release would have been expected since the quantities of urea liberated by the shrimp were approximately equal to those of ammonia.

It is important to note that since experiment 3 was conducted at a temperature 2.5°C lower than the other experiments, a correction of the measured rates should be made in order to compare them properly. Since an appropriate Q_{10} value was not available, the correction was not made. Presumably, however, a Q_{10} for an ammonia release rate would be similar if not identical to that for urea, and the ammonia-urea ratio would not be changed with a temperature correction. The lack of both a temperature correction and an appropriate relationship between body size and nitrogen excretion also makes the comparison of data between different species difficult.

The *E. ringens* experiments produced the highest release rates (particularly for creatine) and the lowest ammonia-urea ratios. This can probably be attributed to the high level of activity and/or the poor health of the specimens.

Wood (1958) ran experiments for 24 hr at 12°C, and from his Table 2 and an approximation of 28% wet weight = dry weight, one can calculate ammonia and urea release rates. These calculated mean release rates are 0.0141, 0.0179, and 0.0065 μg at ammonia-N + urea-N/mg dry weight/day, for the sculpin (*Leptocottus armatus*), the starry flounder (*Platichthys stellatus*), and the blue sea perch (*Taeniotoca lateralis*) respectively. These rates are nearly an order of magnitude lower than those reported here, but a temperature correction (assuming a Q_{10} of 2) would bring them within approximately a factor of five. The calculated ammonia-urea ratios for the sculpin, the starry flounder, and the blue sea perch are 3.09, 7.13, and 1.26 respectively. Since the fish used in Wood's studies were nearly ten times larger than the anchovies, were maintained for some time prior to the experiments on a diet of lingcod muscle, and for the experiments were enclosed in chambers barely larger than the fish, it is difficult to compare the results of the different sets of data.

Ammonia and urea are important plant nutrients and it is of interest to examine the significance of fish excretion as a source of these substances in the sea. Whitledge and Packard (1971) estimated that nitrogen excretion by the herbivorous *E. ringens* in the near surface waters of the Peru Current is an order of magnitude greater per unit volume of water than zooplankton excretion and they suggested, on the basis of these rates and measured rates of nitrogen uptake by phytoplankton, that fish excretion may be a major source of the ammonia utilized by phytoplankton in this area.

Off the coast of southern California the contribution of the fish community in the regeneration of ammonia and urea can also be estimated. Integrated values of phytoplankton nitrogen utilization at three stations in the euphotic zone off the coast of San Diego (Stations 1, 4, and 6, McCarthy[4] averaged 0.073 μg at ammonia-N/liter/day and 0.066 μg at urea-N/liter/day. For the area included in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey, the total biomass of the most common species of near-surface fish [northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), Pacific saury (*Cololabis saira*), and al-

[4] McCarthy, J. J. The uptake of urea by natural populations of marine phytoplankton. Manuscript in preparation.

bacore (*Thunnus alalunga*)] is estimated at 20-25 $\times$ 10^6 metric tons wet weight (Dr. P. E. Smith, personal communication). Using an area of 70 $\times$ $10^{10}m^2$, a depth of 140 m, an average excretion rate from Table 1 (*E. mordax*, experiments 1 and 2, and *T. symmetricus*), and a conversion factor (dry wt = 28% wet wt) approximate production rates of 0.0075 μg at ammonia-N/liter/day and 0.0015 μg at urea-N/liter/day can be calculated. These rates would account for 10% of the ammonia and 2% of the urea utilized by the phytoplankton.

Other investigators—Harris, 1959; Dugdale and Goering, 1967 and 1970; and Martin, 1968—have attempted to balance ammonia utilization by phytoplankton and excretion by zooplankton in Long Island Sound, the Bermuda region, the Peru Current and Narragansett Bay respectively. Further calculations can be made for the area off southern California to compare the significance of fish ammonia and urea excretion to that of zooplankton. A zooplankton standing crop estimate of 0.125 mg dry wt/liter was calculated from 10 years of data collected in the California Current as part of the CalCOFI program by multiplying the mean catch by a factor of 3 to compensate for the biomass of the smaller zooplankton lost through the 0.505 mm mesh (Dr. P. E. Smith, personal communication). Using average excretion rates for recently fed zooplankton (*Calanus helgolandicus, Calanus chilenis*, and *Clausocalanus* sp.) of 0.73 μg at ammonia-N/mg dry wt/day and 0.36 μg at urea-N/mg dry wt/day (McCarthy, 1971) average regeneration rates of 0.090 μg at ammonia/liter/day and 0.045 μg at urea-N/liter/day can be calculated. These rates would account for 123% of the ammonia and 68% of the urea utilized per day. If on the other hand, microzooplankton and zooplankton biomass data collected from April through September 1967 in the same approximate area as two of the three stations used for the phytoplankton utilization calculations are applied (Beers and Stewart, 1970; Mullin and Brooks, 1970) the calculated regeneration would be 0.020 μg at ammonia-N/liter/day and 0.010 μg at urea-N/liter/day. These rates account for 27% of the ammonia and 15% of the urea utilized by the phytoplankton. Hence, the fish contribution would amount to 8-27% of the ammonia and 3-13% of the urea released by both groups of organisms. There undoubtedly are, however, situations in which large fish or schools of fish (the mean density of an *E. mordax* school is estimated as the equivalent of 1,300 10-cm fish/m^3, Dr. P. E. Smith, personal communication) are more important than zooplankton in supplying ammonia and urea to a particular parcel of water.

Obviously these calculations are based on many simplified assumptions. Other than the fact that the zooplankton and fish biomass estimates are averages for larger areas and longer periods of time than can be represented by the phytoplankton utilization rates, perhaps the most poorly based assumption is the application of mean excretion rates for three zooplankton species and two fish species to the entire zooplankton and fish populations. More reliable estimates of excretion rates are needed for smaller species of zooplankton and larger species of fish.

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ELECTROPHORETIC INVESTIGATION OF THE FAMILY SCORPAENIDAE

ALLYN G. JOHNSON, FRED M. UTTER, AND HAROLD O. HODGINS[1]

ABSTRACT

Thirty-one species of three genera of the family Scorpaenidae were separated into 17 groups based on starch gel electrophoretic comparison of muscle proteins and six enzymatic systems. This study concluded that relatively greater similarity existed between the Pacific *Sebastes* and the Atlantic *Sebastes* than between either and the other genera. Ten of the 27 species of Pacific *Sebastes* tested had unique biochemical profiles which may be useful for identification of specimens.

The family Scorpaenidae contains several genera in the Pacific and Atlantic Oceans. On the Pacific coast of North America there are four genera—*Sebastes*,[2] *Sebastolobus*, *Scorpaena*, and *Scorpaenodes*. *The genus of Pacific Sebastes* contains over 50 species (Tsuyuki et al., 1968). In this genus new species and extensions of known distribution ranges have been described in recent years (Westrheim, 1965; Westrheim and Tsuyuki, 1967; Nishimoto, 1970; Tsuyuki and Westrheim, 1970). At present there are difficulties in showing taxonomic relations and, in some instances, in making positive identification of specimens using morphometric and meristic methods, although taxonomic relations can be obtained by biochemical methods. Starch gel electrophoresis—developed by Smithies (1955)—coupled with histochemical procedures (Hunter and Markert, 1957) is one of the best biochemical techniques for taxonomic studies.

Scorpaenid muscle proteins and hemoglobin were investigated by starch gel electrophoresis by Tsuyuki et al. (1968). They suggested that the electrophoretic evidence did not support the separation of the two genera *Sebastodes* and *Sebastes*. Chu (1968), using disk electrophoresis of muscle proteins, found different patterns in two out of eight species of *Sebastodes*. Altukhov and Nefyodov (1968) demonstrated serum protein differences between *Sebastes marinus* and *S. mentella* using agar gel electrophoresis.

This paper reports the findings of our investigation of proteins and six enzyme systems found in the skeletal muscle or liver of members of the family Scorpaenidae. Our study involved 27 species of Pacific *Sebastes*, 2 of the Atlantic *Sebastes*, and 1 each of *Sebastolobus* and *Helicolenus*. We present information on the relative biochemical similarity between genera and a key which separates 10 of the 27 Pacific *Sebastes* species studied. This was not a genetic study per se but a research which demonstrated repeatable biochemical differences between species. The observed constancy of biochemical characters examined within a species in samples taken at different ages, depths, and geographic locations is evidence that the reported differences between species are, indeed, genetic. Alternate explanations for such repeatable expression of proteins under the above conditions seem much less likely.

MATERIAL AND METHODS

Sampling data including location, species, and number of individuals collected are given in Table 1.

Most samples were frozen quickly after capture, but in some instances were kept on ice for short periods; all samples were kept frozen at —20°C after receipt at the laboratory until tested. Extracts were prepared by mixing equal

[1] National Marine Fisheries Service, Northwest Fisheries Center, Seattle Laboratory, 2725 Montlake Boulevard East, Seattle, WA 98102.

[2] In this paper we follow the designation of Bailey (1970) and Chen (1971), considering *Sebastodes* as *Sebastes*. Members of the genus *Sebastes* that were collected along the Pacific Coast of North America are signified in this paper as Pacific *Sebastes*.

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TABLE 1.—Location and number of specimens of Scorpaenidae collected, 1968-70.

Species	Location[1]						Total number of fish
	A	B	C	D	E	F	
Pacific *Sebastes*							
S. aleutianus	10	--	6	--	--	--	16
S. alutus	217	--	843	--	--	--	1,060
S. auriculatus	--	76	--	--	--	--	76
S. aurora	3	--	--	--	--	--	3
S. brevispinis	5	--	40	--	--	--	45
S. caenaematicus	--	--	--	--	--	3	3
S. caurinus	--	283	--	--	--	--	283
S. chlorostictus	--	--	--	--	1	--	1
S. crameri	2	--	16	--	--	--	18
S. diploproa	14	--	--	--	--	--	14
S. elongatus	--	297	96	--	--	--	393
S. entomelas	2	--	2	--	--	--	4
S. flavidus	8	--	--	--	--	--	8
S. helvomaculatus	5	--	19	--	--	--	24
S. levis	--	--	--	--	1	--	1
S. maliger	--	25	--	--	--	--	25
S. melanops	--	28	--	--	--	--	28
S. paucispinis	2	--	15	--	1	--	18
S. pinniger	--	--	24	--	--	--	24
S. proriger	9	--	100	--	--	--	109
S. reedi	1	--	110	--	--	--	111
S. ruberrimus	5	27	5	--	--	--	37
S. rubivinctus	5	--	34	--	--	--	39
S. saxicola	5	--	--	--	1	--	6
S. wilsoni	--	--	1	--	--	--	1
S. variegatus	--	--	--	--	--	1	1
S. zacentrus	1	--	37	--	--	--	38
Atlantic *Sebastes*							
S. marinus	--	--	--	9	--	--	9
S. viviparous	--	--	--	10	--	--	10
Sebastolobus alascanus	--	--	100	--	--	--	100
Helicolenus dactylopterus	--	--	--	10	--	--	10

[1] A = Pacific Coast of Washington and Oregon, 1968-70; B = Puget Sound, Wash., 1968-70; C = Queen Charlotte Sound, B.C., Canada, June 1970; D = West Coast of Britain and Ireland, August 1970; E = Avila Beach, Calif., October 1970; F = Cape Ommaney, Alaska, April 1970.

volumes of tissue and phosphate-buffered physiological saline solution (pH 7.4) into uniform pastes with glass rods. The extracts were tested by electrophoresis without further treatment by (1) drawing them into ¼-inch × 3/16-inch filter paper inserts (Schleicher and Schuell grade S and S No. 470)[3], placed on the surface of the tissue-saline mixture, and (2) placing the inserts into starch gels.

Electrophoresis in starch gel followed the methods of Kristjansson (1963). All but two of the biochemical systems were resolved well using a buffer system described by Markert and Faulhaber (1965). Lactate dehydrogenase and phosphoglucomutase were best resolved by using the buffer system described by Ridgway, Sherburne, and Lewis (1970). Gels consisted of 35 g starch plus 250 ml of buffer. A voltage of 300 was applied for 10 min; sample inserts were removed and 400 v applied until indicator dye markers reached a point 6 to 9 cm anodal to the origin. The gels were cooled during electrophoresis by placing ice packs on glass plates on top of the gels. After electrophoresis, bands reflecting enzyme activity were detected by the following methods:

Tetrazolium oxidase (TO) (after Brewer, 1967, and Johnson, Utter, and Hodgins, 1970b):
- 5 mg phenazine methosulfate (PMS)
- 3 mg p-nitro blue tetrazolium (NBT)
- 40 ml tris-citrate buffer (0.03 M tris, 0.005 M citric acid, pH7.0)

L-alpha-glycerophosphate dehydrogenase (αGPDH) (after Nyman, 1967, and Johnson, Utter, and Hodgins, 1970a):
- 5 mg PMS
- 3 mg NBT
- 5 mg NAD+
- 100 mg L-alpha-glycerophosphate
- 40 ml tris-citrate buffer

Lactate dehydrogenase (LDH):
- 10 mg PMS
- 5 mg NBT
- 5 mg NAD+
- 20 ml of 0.5 M sodium lactate solution
- 40 ml tris-citrate buffer

Peptidase A (after Lewis and Harris, 1967, and Lewis and Truslove, 1969):
- 10 mg DL valyl-leucine
- 1 mg horseradish peroxidase
- 5 mg 0-dianisidine in 10 ml acetone
- 0.5 ml M $MgCl_2$
- 1 mg *Bothrops atrox* venom
- 40 ml tris-citrate buffer

Phosphoglucomutase (PGM) (after Spencer, Hopkinson, and Harris, 1964):
- 100 mg glucose-1-phosphate (dipotassium salt)
- 5 mg NADP
- 5 mg PMS
- 3 mg NBT
- 20 units glucose-6-phosphate dehydrogenase

[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

TABLE 2.—Classification of species of Scorpaenidae into various groups by means of biochemical characteristics.

Species	Biochemical characteristics						Biochemical group
	Muscle pattern[1]	TO	GPDH	LDH	Peptidase A		
					I (Fast zone)	II (Slow zone)	
Pacific *Sebastes*							
S. elongatus	2	F	E	C	c	c	I[2]
S. entomelas	2	S	E	C	c	c	II[2]
S. aurora	3	F	E	C	b	d	III[2]
S. chlorostictus	4	F	E	B	a	c	IV[2]
S. aleutianus	4	F	E	C	c	c	V
S. zacentrus	4	F	E	C	c	c	V
S. caurinus	4	F	F, S	C	d	c	VI
S. diploproa	4	F	E	C	b	b	VII[2]
S. helvomaculatus	4	F	E	B	c	c	VIII[2]
S. maliger	4	F	F	C	d	c	VI
S. ruberrimus	4	F	E	C	c	c	V
S. rubrivinctus	4	F	E	C	c	c	V
S. saxicola	4	F	F	C	c	c	IX[2]
S. auriculatus	4	F	E, F	C	d	c	VI
S. brevispinis	4	F	E	C	c	c	V
S. flavidus	4	S	E	C	c	c	X
S. melanops	4	S	E	C	c	c	X
S. pinniger	4	S	E	C	c	c	X
S. proriger	4	S	E	C	c	c	X
S. wilsoni	4	S	--	--	--	--	--
S. variegatus	4	S	E	C	a	c	XI[2]
S. caenaematicus	4	S	E	C	c	c	X
S. alutus	4	S	F, S	C	c	c	XII[2]
S. crameri	4	VS	E	C	c	c	XIII
S. paucispinis	4	VS	E	C	c	c	XIII
S. reedi	4	VS	E	C	c	c	XIII
S. levis	—[3]	F	E	C	a	c	XIV[2]
Sebastolobus alascanus	A	VS	D	A	b	a, e	XV[2]
Atlantic *Sebastes*							
S. marinus	B	S	E, F	B	c	c	XVI
S. viviparous	B	S	E	B	c	c	XVI
Helicolenus dactylopterus	G	S, VS	C	B	e	b	XVII[2]

[1] Modified after Tsuyuki et al., 1968.
[2] Species with unique biological characteristics.
[3] Pattern of the single specimen tested has not been described.

0.5 ml 1 M $MgCl_2$
40 ml tris-citrate buffer

Isocitrate dehydrogenase (ICDH):

(a) NADP dependent (after Opher, Leonard, and Miller, 1969):
30 mg DL sodium isocitrate
5 mg NADP
0.5 ml 1 M $MgCl_2$
5 mg PMS
5 mg NBT
40 ml tris-citrate buffer

(b) NAD + dependent:
Same formulation as NADP dependent, but substituting 10 mg NAD + for 5 mg NADP

Muscle protein detected by nonspecific protein staining using 1% nigrosin-buffalo black in solution of 1:4:5 acetic acid:methanol:water and destained with a 1:4:5 solution of acetic acid, methanol, and water.

ENZYME AND PROTEIN PHENOTYPES

TETRAZOLIUM OXIDASE (TO)

Interspecific variation of TO was previously reported in the genus *Sebastes* (Pacific) by Johnson et al. (1970b), where three anodal mobilities were observed in 15 species studied: Fast (F), Slow (S), and Very Slow (VS). These findings are expanded in the present study (Table 2, Figure 1). The F band occurred in 15 of the 27 Pacific *Sebastes* species; the S band was present in 9 species and the VS band in 3 species. Only the S band occurred in both Atlantic *Sebastes* species. The VS band was found

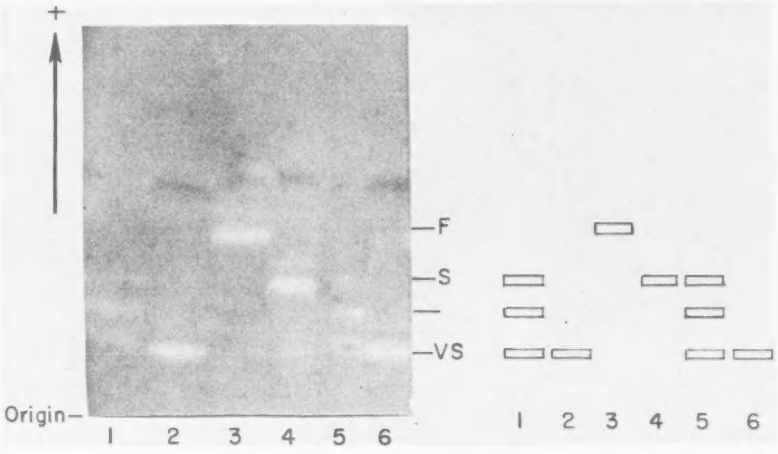

FIGURE 1.—Band in starch-gel illustrating the four tetrazolium oxidase phenotypes, F, S, S-VS, and VS, detected in the family Scorpaenidae. The following samples are shown: 1, 5 *Helicolenus dactylopterus* (S-VS), 2 *Sebastes reedi* (VS), 3 *Sebastes caurinus* (F), 4 *Sebastes alutus* (S), and 6 *Sebastes reedi* (VS).

in *Sebastolobus alascanus*.[4] *Helicolenus dactylopterus* was polymorphic for the S and VS bands; of the 10 samples tested, two exhibited a three-banded phenotype having the S and VS bands in addition to another band of intermediate mobility, whereas the rest had only the single S band. The three-banded phenotype suggests that two TO alleles are segregating in *Helicolenus* and that tetrazolium oxidase functions as a dimer in scorpaenids. This interpretation is consistent with TO polymorphisms observed in salmonids (Utter, 1971) where three-banded phenotypes were observed in heterozygous rainbow trout (*Salmo gairdneri*) and chinook salmon (*Oncorhynchus tshawytscha*).

L-ALPHA -GLYCEROPHOSPHATE DEHYDROGENASE (αGPDH)

Evidence for a polymorphic dimer having two alleles—Fast (F) and Slow (S)—were described in *S. alutus* (Johnson et al., 1970a). In addition to the F and S bands, three faster αGPDH bands have been observed among the scorpaenids that we have tested: E, D, and C,[5] listed according to increasing mobility (Figure 2 and Table 2). Additional αGPDH bands invariably occurred, regardless of phenotype, when electrophoresis proceeded beyond a 6-cm anodal migration of the dye marker. These bands are presumably artifacts of electrophoresis and did not alter our interpretation of enzyme variations. This phenomenon was also noticed by McCabe, Dean, and Olson (1970) in αGPDH variants of skipjack tuna (*Katsuwonus pelamis*).

In Pacific *Sebastes*, 19 species were monomorphic for the E band. *S. auriculatus* was polymorphic for the E and F bands. *S. caurinus* as well as *S. alutus* were polymorphic for F and S bands. *S. maliger* and *S. saxicola* were monomorphic for the F band. In the Atlantic *Sebastes*, *S. viviparous* was monomorphic for the E band and *S. marinus* was polymorphic for the E and F bands. The D and C bands were monomorphic *Sebastolobus alascanus* and *Helicolenus dactylopterus*, respectively.

[4] We used liver extracts of this species for detection of TO activity because muscle extracts failed to develop TO bands. We assume that this is a valid comparison because of parallel TO activity between liver and muscle observed in other scorpaenid species. All other scorpaenid enzymes tested were extracted from skeletal muscle.

[5] The separation of αGPDH bands C and D depends on optimal electrophoretic conditions.

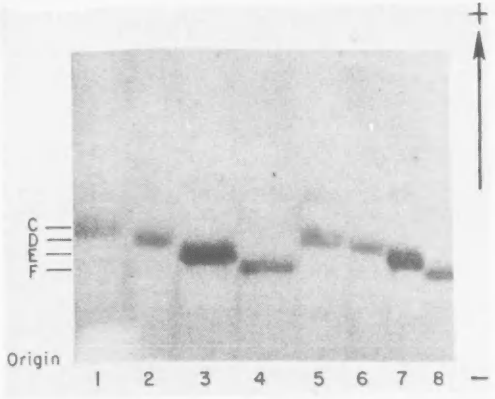

FIGURE 2.—Bands in starch-gel illustrating four L-alpha glycerophosphate dehydrogenase phenotypes (C, D. E, F) detected in the family Scorpaenidae. The following samples are shown: 1, 5 *Helicolenus dactylopterus* (C), 2, 6 *Sebastolobus alascanus* (D), 3, 7 *Sebastes rubrivinctus* (E), and 4, 8 *Sebastes alutus* (F).

LACTIC DEHYDROGENASE (LDH)

Muscle LDH was resolved as a single anodal band in each scorpaenid species we tested. This agrees with studies of Wilson, Kitto, and Kaplan (1967), who found single anodal bands of muscle LDH in two scorpaenid species, *Sebastes marinus* and *Scorpaenopsis gibbosa*. The electrophoretic mobilities were distinct in each species. LDH bands of three different mobilities (A, B, and C) were found in our sampling (Figure 3 and Table 2). No polymorphisms were detected. All but two Pacific *Sebastes* species expressed the C band. The B band was found in *S. helvomaculatus* and *S. chlorostictus*. The B band was found in two Atlantic *Sebastes* species and *Helicolenus dactylopterus*. Only *Sebastolobus alascanus* expresses the LDH A band.

PEPTIDASE

Peptidase staining occurred in two anodal regions for all species tested (Figure 4, Table 2). Both regions are developed with the dipeptide valyl-leucine, which is the specific substrate for peptidase A in mammals (Lewis and Harris, 1967; Lewis and Truslove, 1969). We have therefore called these regions peptidase A-I and peptidase A-II.

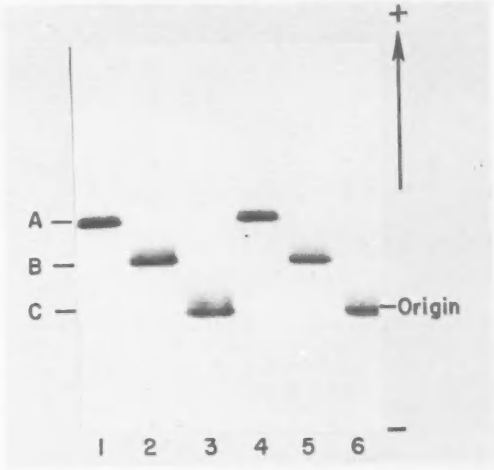

FIGURE 3.—Bands in starch-gel illustrating the three phenotypes of lactate dehydrogenase detected in the family Scorpaenidae. The following species are shown: 1, 4 *Sebastolobus alascanus* (A), 2, 5 *Sebastes helvomaculatus* (B), and 3, 6 *Sebastes alutus*.

Five different bands (a, b, c, d, e) were observed in the peptidase A-I (fast) zone. In Pacific *Sebastes*, peptidase A-I bands were expressed as follows: I^a - *S. chlorostictus, S. levis,* and *S. variegatus*; I^b - *S. caurinus, S. auriculatus,* and *S. maliger*. *S. marinus* had band I^c as did 9 of the 10 *S. viviparous* tested; *Sebastolobus alascanus* had band I^b; and *H. dactylopterus* had band I^e. The aberrant *Sebastes viviparous* sample had a single I^d band but corresponded to *S. viviparous* in all other systems tested. The significance of the variant is unclear. It may reflect an intraspecies genetic variant (although multiple bands would be expected if this were the case) or perhaps a sibling species. Because only muscle samples were available for Atlantic *Sebastes*, identification of subtle morphological differences between individuals was not possible.

Bands of five different mobilities (a, b, c, d, e) were also observed in the peptidase A-II (slow) zone. Band II^c was expressed in all but two Pacific *Sebastes* tested; band II^d was found in *S.*

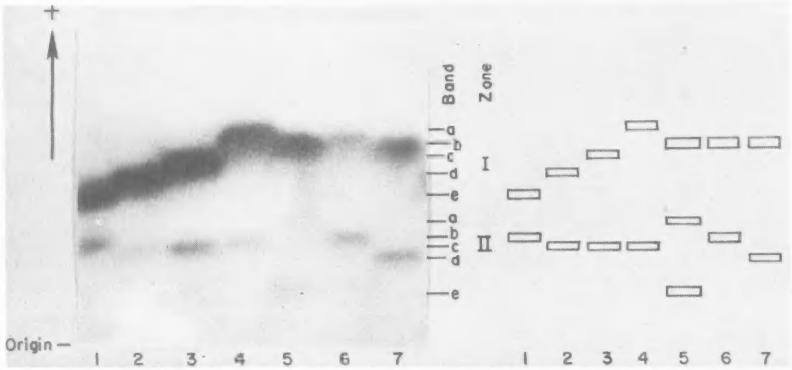

FIGURE 4.—Bands in starch-gel illustrating the various phenotypes of Peptidase A detected in the family Scorpaenidae. The following species are shown: 1 *Helicolenus dactylopterus* (II^b, I^e), 2 *Sebastes caurinus* (II^d, I^c), 4 *Sebastes variegatus* (II^c, I^a), 5 *Sebastologus alascanus* ($II^{a,e}$ I^b), 6 *Sebastes diploproa* (II^b, I^b), and 7 *Sebastes aurora* (II^d, I^b).

aurora and band II^b in *S. diploproa*. Band II^c was found in both Atlantic *Sebastes* species, and *Helicolenus dactylopterus* possessed band II^b. Two bands representing the extremes of peptidase A-II mobilities—II^a and II^e—were expressed in all *Sebastolobus alascanus* individuals tested. These bands are presumed to be fixed rather than polymorphic because of their invariant expression and may reflect gene duplication.

PHOSPHOGLUCOMUTASE (PGM)

PGM polymorphism was reported in *Sebastes alutus*, where two allelic bands—A and B—were described (Johnson, Utter, and Hodgins, 1971). In extending these observations here to additional scorpaenid species a third band—A′—has also been found which migrates somewhat faster than the A band (Figure 5).

PGM is the most polymorphic of the scorpaenid enzymes that we have investigated (Table 3). In Pacific *Sebastes* polymorphism was found in 10 species for the A and B bands and in 1 species for the A and A′ bands. Twelve species of Pacific *Sebastes* were monomorphic for the A band, one for the B band, and one for the A′ band. In other scorpaenid species, *Sebastes marinus* was polymorphic for the A and B bands, and *S. viviparous* was monomorphic for

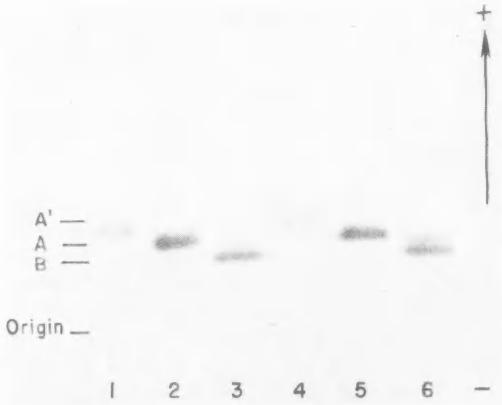

FIGURE 5.—Bands in starch-gel illustrating three mobilities of phosphoglucomutase detected in the family Scorpaenidae. The following species are shown: 1, 4 *Sebastolobus alascanus* (A′), 2, 5 *Sebastes caurinus* (A), and 4, 6 *Sebastes reedi* (B).

the A band. *H. dactylopterus* was polymorphic for the A and B bands, and *Sebastolobus alascanus* was monomorphic for the A′ band. We assume that these variants reflect allelic differences although further study is needed for some species. Also, the limited number of samples

tested for some species that were listed as monomorphic are too few to preclude the possibility of polymorphism.

ISOCITRATE DEHYDROGENASE, NADP DEPENDENT (ICDH NADP)

We tested for both NAD- and NADP-dependent ICDH in the 31 species studied and found activity only for the latter form. It is assumed that this represents cytoplasmic ICDH activity (Opher et al., 1969). Two anodal mobilities of ICDH were detected: the band of *H. dactylopterus* migrated slightly faster than the band of the other species (Figure 6). No activity was detectable in extracts of *Sebastolobus alascanus*. Activity was highly labile in all species, requiring testing on the same day that the extraction was made. It may be that *S. alascanus* has an even more labile form of ICDH than the other species tested.

TABLE 3.—Phosphoglucomutase phenotypes in muscle samples from species of Scorpaenidae.[1]

Species	Phenotypes				
	B	AB	A	AA'	A'
Pacific *Sebastes*					
S. aleutianus	--	+	+	--	--
S. alutus	+	+	+	--	--
S. auriculatus	--	--	+	--	--
S. aurora	--	+	+	--	--
S. brevispinis	+	+	+	--	--
S. caurinus	--	--	+	--	--
S. chlorostictus	--	--	--	--	+
S. crameri	--	+	+	--	--
S. elongatus	+	+	+	--	--
S. entomelas	--	--	+	--	--
S. flavidus	--	--	+	--	--
S. helvomaculatus	--	--	+	+	+
S. levis	--	--	+	--	--
S. maliger	--	--	+	--	--
S. melanops	--	--	+	--	--
S. paucispinis	--	+	+	--	--
S. pinniger	--	+	+	--	--
S. proriger	+	+	+	--	--
S. reedi	+	--	--	--	--
S. ruberrimus	--	--	+	--	--
S. rubivinctus	--	--	+	--	--
S. saxicola	--	--	+	--	--
S. zacentrus	--	--	+	--	--
S. caenaematicus	--	+	+	--	--
S. variegatus	--	--	+	--	--
Atlantic *Sebastes*					
S. marinus	--	+	+	--	--
S. viviparous	--	--	+	--	--
Sebastolobus alascanus	--	--	--	--	+
Helicolenus dactylopterus	+	--	+	--	--

[1] PGM in our samples of *S. diploproa* and *S. wilsoni* did not develop.

FIGURE 6.—Isocitric dehydrogenase (NADP dependent) bands found in the family Scorpaenidae. Samples 1, 3, 5 are *Sebastes alutus* and samples 2, 4 are *Helicolenus dactylopterus*.

MUSCLE PROTEIN

A satisfactory separation of muscle protein bands was obtained by permitting the dye marker to migrate 9.0 cm anodally from the origin. These bands were separated into two regions—A and B (Figure 7).

Distinct protein patterns occurred in region A, which differ between genera as well as within the genus *Sebastes* (Pacific) (Table 4). *S. aurora* has a unique pattern (bands 1, 4) which differed from the other Pacific *Sebastes* species (bands 1, 3). The intergeneric differences in region A were: *Sebastes* (Pacific)—bands 1, 4 and 1, 3; *Sebastes* (Atlantic)—bands 2, 6; *Helicolenus*—bands 3, 7; and *Sebastologus*—5, 7. A band (X) which migrated more anodally than band 7 was found in some *Sebastes alutus*. We assume this band (X) to be an artifact as it did not appear in repeated tests. The most anodal band (8) was found in all samples tested. Corresponding region A patterns were not described by Tsuyuki et al. (1968) in instances where the same species were tested and may arise from differences in methodology such as buffer systems (Rasmussen, 1969).

TABLE 4.—Intergeneric comparison of muscle protein bands of Scorpaenids.

Genus	Subgroup[1]	Protein bands																					
		Region B[2]															Region A						
		a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	1	2	3	4	5	6	7	8
Pacific *Sebastes*	2	+	+	+	--	--	--	--	--	--	+	+	--	+	--	--	+	+	--	+	--	--	--	--	+
Pacific *Sebastes*	3	--	--	--	--	--	+	--	+	--	--	+	--	+	--	--	+	+	--	--	+	--	--	--	+
Pacific *Sebastes*	4	+	+	+	--	--	--	--	--	+	--	+	--	+	--	--	+	+	--	+	--	--	--	--	+
Atlantic *Sebastes*	--	+	+	+	--	--	--	--	--	+	--	+	--	+	--	--	+	--	+	--	--	--	+	--	+
Sebastolobus	--	--	--	--	--	--	--	--	--	+	--	--	+	--	--	+	--	--	--	--	--	+	--	+	+
Helicolenus	--	+	+	+	--	--	--	--	--	+	--	+	--	+	--	--	+	--	--	--	--	--	--	+	+

[1] Pacific *Sebastes* subgroups after Tsuyuki et al., 1968.
[2] Alphabetical classification after Tsuyuki et al., 1968.

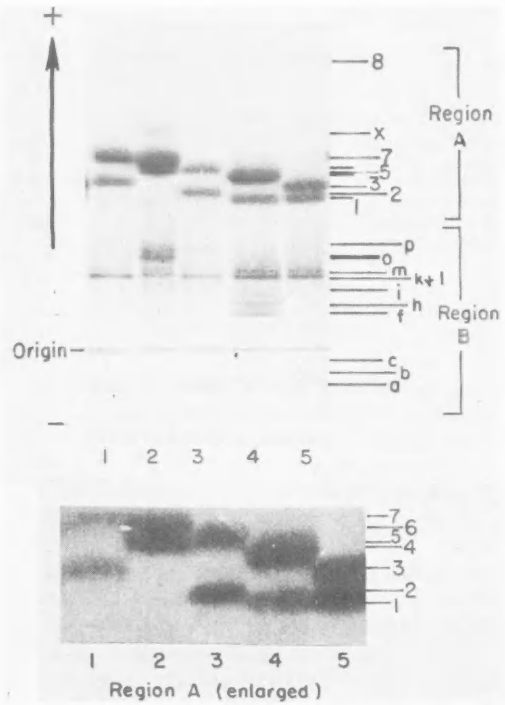

FIGURE 7.—Muscle protein bands in starch-gel: 1 *Helicolenus dactylopterus* (A-3, 7), 2 *Sebastolobus alascanus* (A-5, 7), *Sebastes marinus* (A-2, 6), 4 *Sebastes aurora* (A-1, 4), and 5 *Sebastes alutus* (A-1, 3).

The protein patterns in region B were similar to those described by Tsuyuki et al. (1968), who described 16 bands (a-p) that varied between genera and species. Three cathodally migrating bands (a, b, c) occurred in Pacific *Sebastes* (except *S. aurora*), Atlantic *Sebastes*, and *Helicolenus*. Bands b and c stained weakly in our gels and failed to show in some individuals (Figure 7). The slowest anodal bands were f and h which occurred only in *S. aurora*. Band i occurred in all species tested except *S. aurora*, *S. elongatus*, and *S. entomelas*. On the other hand, *S. entomelas* and *S. elongatus* were the only species having the j band, bands j and k being polymorphic in *S. elongatus* (first reported by Tsuyuki et al., 1968). Band k was present in all genera but *Sebastolobus*, which—in turn—was the only genus expressing band l. Similarly, bands m and p—present in other genera—were absent in *Sebastolobus*, which uniquely expressed band o. Our methods were unable to detect band q, reported by Tsuyuki et al. in Atlantic *Sebastes* and *Sebastolobus*.

COMPARISON OF VARIATION BETWEEN GENERA

A comparison of the total variation between genera suggests some possible relations. The greatest similarity was between the Pacific *Sebastes* and Atlantic *Sebastes* where all the electrophoretic patterns of the Atlantic *Sebastes* were found in one or more species of the Pacific *Sebastes*, except for the protein bands of region A. Pacific *Sebastes* and *Sebastolobus* exhibited common bands for PGM, TO, peptidase A-I, and protein B-i. Pacific *Sebastes* and *Helicolenus* shared common bands for LDH, PGM, and protein bands of region B. *Helicolenus* and one species of Pacific *Sebastes* possessed a common peptidase A-II band. *Helicolenus* and *Sebastes* had common bands in LDH, PGM, and protein region B. *Helicolenus* and *Sebastolobus* shared only pro-

tein bands B-i and A-7. Only protein band B-i was common to *Sebastolobus* and the Atlantic *Sebastes* (Tables 2, 4, and 5).

When the total amount of common patterns between genera is considered, we agree with Tsuyuki et al. (1968) that there is relatively greater similarity between the Pacific *Sebastes* and the Atlantic *Sebastes* than between either and the other genera studied. *S. aurora* was found to have relatively the same degree of difference between itself and the other Pacific *Sebastes* species as there was between the Atlantic *Sebastes* and the Pacific *Sebastes*. This agrees with the findings of Tsuyuki et al. (1968) who suggested that *S. aurora* should possibly be elevated to the generic level because of its degrees of difference. The interpretation of similarity based on electropherograms must be done with caution as only amino acid substitutions which change the net charge of the polypeptide chain can be detected.

TABLE 5.—Summary of intergeneric enzymatic similarity in Scorpaenidae.[1] X indicates the occurrence of common bands between one or more species of the genera compared.

Genus and enzyme	Genera			
	Pacific *Sebastes*	Atlantic *Sebastes*	*Sebastolobus*	*Helicolenus*
Pacific *Sebastes*				
TO		X	X	--
αGDPH		X	--	--
LDH		X	--	X
Peptidase A-I		X	X	--
Peptidase A-II		X	--	X
ICDH		X	--	--
PGM		X	X	X
Atlantic *Sebastes*				
TO	X		--	--
αGDPH	X		--	--
LDH	X		--	X
Peptidase A-I	X		--	--
Peptidase A-II	X		--	--
ICDH	X		--	--
PGM	X		--	X

[1] No common bands were found between *Sebastolobus* and *Helicolenus*.

VARIATION WITHIN PACIFIC *SEBASTES*

Combining the enzyme and protein variations in the Pacific *Sebastes* resulted in 10 of the 27 Pacific *Sebastes* species having unique biochemical profiles (Table 2). These species were *S. elongatus*, *S. entomelas*, *S. aurora*, *S. chlorostictus*, *S. diploproa*, *S. helvomaculatus*, *S. saxicola*, *S. variegatus*, *S. alutus*, and *S. levis*. Some species were represented by only a few samples —therefore further sampling may reveal variation in these profiles. PGM was not included in these profiles because of its high degree of polymorphism in the genus. A new species, *S. reedi*, was reported by Westrheim and Tsuyuki (1967) that resembles *S. crameri*, *S. alutus*, and *S. proriger* but was readily separable from these when morphology and biochemical methods were employed. Our study found that *S. reedi* and *S. crameri* were identical with respect to muscle protein and five enzyme systems but differed in PGM. This suggests that *S. reedi* may be more closely related to *S. crameri* than to the other species.

Three species, *S. caurinus*, *S. maliger*, and *S. auriculatus*, had profiles that differed only in the enzyme αGPDH, which was monomorphic in *S. maliger* (F band) but polymorphic for the F and S bands in *S. caurinus*. All three species have the peptidase A-I[d] band which was found in no other *Sebastes* species. These three species are very similar in morphology and habitat preferences. In certain areas of Puget Sound, Wash., hybridization between the three may occur, whereas in other areas they remain separate because of behavioral differences.[6] Investigation of biochemical and morphological characteristics of these species may provide valuable information on the processes of speciation.

The amount of polymorphism of αGPDH and PGM in the family Scorpaenidae could prove to be useful for the identification of breeding populations and verification of species and subspecies. On the basis of morphometric data, Barsukov (1964) suggested that two subspecies exist in *Sebastes alutus* (*S. a. alutus*—off the Pacific coast of North America and *S. a. paucispinus*—from Honshu Island, Japan, to perhaps Bristol Bay, Alaska). Westrheim (1970) suggested that *S. alutus* had a southern and a northern type of fish off the coast of North America—the south-

[6] C. R. Hitz, National Marine Fisheries Service, Fishery Biologist, Exploratory Fishing and Gear Research Base, Seattle, Wash., personal commun., April 1971.

ern type south of Dixon Entrance and the northern type North of Dixon Entrance and in the Gulf of Alaska. Differences in gene frequencies would add to the support of their separations. This approach may also prove useful in studying complexes such as found in *S. aleutianus, S. reedi,* and *S. diploproa* (Tsuyuki et al., 1968).

SUMMARY

An investigation of muscle protein and six enzymatic systems by starch-gel electrophoresis was presented. Samples of 31 species of three genera of the family Scorpaenidae were compared which resulted in the conclusion that a relatively greater similarity existed between the Pacific *Sebastes* and the Atlantic *Sebastes* than between the other genera.

Ten of the 27 species of Pacific *Sebastes* had unique profiles when the systems were compared.

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THE SYNERGISTIC EFFECTS OF TEMPERATURE, SALINITY, AND MERCURY ON SURVIVAL AND METABOLISM OF THE ADULT FIDDLER CRAB, *UCA PUGILATOR*[1]

WINONA B. VERNBERG AND JOHN VERNBERG[2]

ABSTRACT

Gill tissues of fiddler crab, *Uca pugilator*, were the major site of mercury concentration; lesser amounts accumulated in the hepatopancreas and green gland. Very small amounts were found in the carapace and muscle tissue. No significant differences in the amount of mercury in tissues of males and females were found.

A concentration of mercury sublethal to fiddler crabs under optimum conditions of temperature and salinity greatly reduced survival times when crabs were placed under conditions of temperature and salinity stress. Males were more susceptible to the synergistic effects of mercury in combination with environmental stress than were females.

Metabolic rates of male and female fiddler crabs were affected by prolonged exposure to mercury both under optimum environmental conditions and under temperature and salinity stress. Metabolic rates of males were more adversely affected than those of females.

Estuaries are an extremely important part of the marine environment. Yet often an estuary becomes so grossly polluted that much of the biota is destroyed before it is recognized that the quality of water affects the biology of such an area. Part of the problem is the subtleness of the effects of sublethal concentrations of man-introduced pollutants. In low concentration the pollutant may have no observable effect on a given population of animals if environmental conditions remain at an optimum. However, when another environmental parameter becomes stressful, it may synergistically interact with the sublethal concentration of pollutant and the organism dies. Many estuaries are polluted, and since one of the chief characteristics of estuaries is the rather extreme environmental fluctuations that occur throughout the year, knowledge of synergistic interaction on estuarine animals is important in the preservation of estuarine ecosystems.

This study was undertaken to determine the effect of a sublethal concentration of mercury on the metabolism of adult male and female fiddler crabs, *Uca pugilator* (Bosc), maintained under optimum and stressful conditions of temperature and salinity, and the synergistic effects on survival of this species with sublethal concentration of mercury in combination with salinity and thermal stress. This species was selected because it is one of the more abundant and ecologically important species in an estuarine ecosystem.

MATERIALS AND METHODS

Crabs used in this study were collected in the Georgetown, S.C., area during the fall and winter months. After collection the animals were brought into the laboratory where they were maintained in plastic boxes containing a thin layer of seawater having a salinity of approximately 30‰. All crabs were kept in constant temperature boxes at 25°C and on a 12-hr light-dark photoperiod for at least 2 weeks. Crabs were fed on Clark's fish pellets every third

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day; the water was changed after each feeding. Preliminary studies were undertaken to determine the amount of $HgCl_2$, an inorganic mercury compound, that could be added to the water without killing the crabs. A concentration of 9×10^{-7} M $HgCl_2$ was found to be sublethal for crabs which were kept under optimal conditions of temperature and salinity. Under these conditions crabs survived for a 2-month period with only slight mortality. The experiment was terminated at this point. The initial concentration of mercury, 9×10^{-7} M $HgCl_2$ was 0.18 ppm Hg (or 0.18 mg/liter seawater).

Tissues of crabs were analyzed for mercury following exposure to 0.18 ppm mercury in 30‰ seawater at a temperature of 25°C for 1, 3, 7, 14, and 28 days. Tissues of crabs maintained under the same conditions but without added mercury were also analyzed. Tissues were removed from 10 crabs for each assay and frozen immediately. The concentration of mercury in each tissue was then determined on a Perkin-Elmer Mercury Analyzer System-50.[3] The techniques were based on the Environmental Protection Agency method developed by the Analytical Quality Control Laboratory, using dilute nitric acid to digest the samples. Determinations were made by South Carolina State Board of Health personnel. Five tissues were assayed: gill, hepatopancreas, green gland, abdominal muscle, and carapace. None of the tissues were kept frozen for more than 1 week. Tissues from 20 males and females (two determinations each) were assayed for each of the five experimental time exposures. Since the amount of mercury proved to be essentially the same in tissues of both males and females, all data were pooled.

To determine the synergistic effects of the normally sublethal concentrations of mercury and stressful environmental factors, crabs acclimated to 25°C, 30‰ seawater were placed in seawater with a salinity of 5‰ containing 0.18 ppm mercury or in 5‰ seawater without mercury and maintained at either 5°C or 35°C. At each experimental temperature, four groups of animals were used. Thus at 5°C, 5‰, one group of 30 males and a second group of 30 females were used as controls; in the experimental group 30 males and 30 females were maintained under the same conditions except the water contained 0.18 ppm mercury. The same procedure was followed at 35°C and in a salinity of 5‰. Survival of both experimental and control crabs was followed for 28 days or until 50% of any one group had died. The temperatures of 5°C and 35°C were selected since they represent low and high temperature extremes which fiddler crabs experience seasonally in South Carolina marshes. A salinity of 5‰ is also encountered by them in the field.

Oxygen consumption of control and experimental animals was determined by means of a Gilson respirometer using respiration flasks with a volume of approximately 140 cc. Base-line oxygen consumption measurements were made on 10 males and 10 females in untreated seawater (30‰) at 25°C. These same crabs were then maintained under the same conditions but with 0.18 ppm Hg added to the water, and metabolic determinations made on days 1, 3, 7, 14, 21, and 28. Only medium-sized crabs in the intermolt stage were used to avoid any variation due to molting or metabolic size relationships.

Oxygen consumption rates were also determined on crabs exposed to mercury in combination with temperature and salinity stress. Metabolic measurements were made on crabs maintained in 5‰ seawater at 5°C (control crabs) and crabs kept in 5‰ seawater at 5°C with 0.18 ppm Hg added to the water (experimental crabs). Oxygen consumption rates were then determined after 1 and 3 days exposure for experimental crabs and 1, 3, and 7 days for control crabs. These conditions proved too stressful for most of the crabs to survive longer periods of time. The same experimental procedures were followed for crabs kept in 5‰ at 35°C with and without added mercury. Since these conditions were less stressful than the combination of low salinity and low temperature, it was possible to measure the metabolic rate of these crabs on days 1, 3, 7, 14, and 21 for experimental animals and to day 28 for control crabs. All results are expressed as μliters of oxygen consumed per hour per gram live weight.

[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

RESULTS

MERCURY UPTAKE BY TISSUE

Mercury was not detected in the untreated seawater, although there were detectable traces of mercury found in the Clark's fish pellets fed to the crabs. The hepatopancreas of the control animals (animals collected in the same region as experimental animals and maintained in seawater without mercury addition) had approximately 0.03 ppm mercury, but no mercury was found in any of the other tissues. Within the first 24 hr after exposure to 30‰ seawater at 25°C containing an initial concentration of 0.18 ppm mercury, however, gill tissue contained 1.73 ppm mercury; the amount of mercury in this tissue increased steadily with continued exposure (Figure 1). Of the five tissues assayed for mercury content, gill tissue was found to have the highest concentration. Mercury also accumulated in the hepatopancreas and green gland although much less rapidly and at a lower concentration level (Figure 1). Lower amounts of mercury were found in abdominal muscle tissues and in the carapace; after 28 days exposure to water containing mercury, levels were approximately 1 ppm.

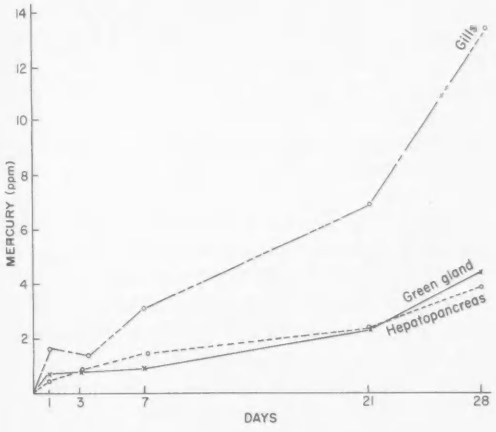

FIGURE 1.—Mercury in tissues of *Uca pugilator* after exposure of the crabs to 9×10^{-7} M $HgCl_2$ (0.18 ppm Hg) in 30‰ seawater at 25°C for varying lengths of time.

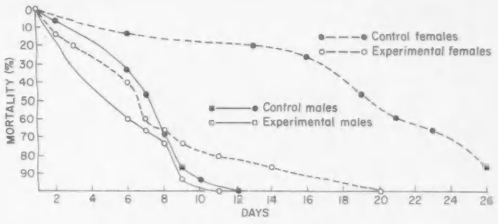

FIGURE 2.—Mortality of *Uca pugilator* in 5‰ seawater at 5° C with and without the addition of 9×10^{-7} M $HgCl_2$ (0.18 ppm Hg).

LETHAL LEVELS

Preliminary studies established that under optimum conditions of temperature (25°C) and salinity (30‰) the crabs could survive for prolonged periods of time (at least 2 months) in seawater having an initial concentration of 9×10^{-7} M $HgCl_2$ (0.18 ppm mercury). Under temperature and salinity stress, however, this concentration of mercury significantly shortened survival time. For example, under conditions of low temperature (5°C) and low salinity (5‰), such as could occur following heavy winter rains, the crabs could not survive as long as under conditions of high temperature and low salinity. In winter animals without the added stress of a pollutant, 50% of the females survived 21 days but 50% of the males were dead within 7 days. Under the same temperature and salinity conditions with the addition of 0.18 ppm mercury, males survived 6 days, but 50% of the females died by day 8 (Figure 2). Under conditions of low salinity (5‰) and high temperature (35°C), conditions very apt to occur following the heavy rains associated with a summer hurricane, both male and female *U. pugilator* can survive with very little mortality for at least 28 days (Figure 3). With the addition of 0.18 ppm mercury, however, survival times of both males and females are reduced. Under conditions where crabs were maintained at this high temperature and low salinity in water containing mercury, 50% of the males had died by day 17, while 50% of the females survived to day 26 (Figure 3).

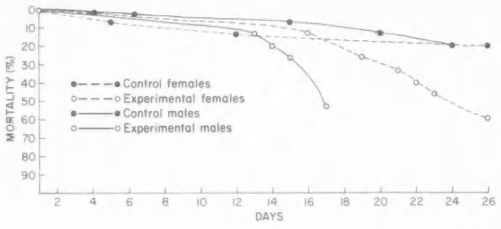

FIGURE 3.—Mortality of *Uca pugilator* in 5‰ seawater at 35°C with and without the addition of 9×10^{-7} M $HgCl_2$ (0.18 ppm Hg).

METABOLIC EFFECTS

Although a low level concentration of mercury was not lethal to the crabs under optimum environmental conditions, metabolic rates of these crabs were affected, especially those of males. Initially, metabolic rates were established for both males and females at 25°C in 30‰ seawater, and the rates for males and females were essentially the same (Figure 4). After the base-line rate was determined, the same animals were then maintained at 25°C in 30‰ seawater with the addition of mercury, and metabolism of the crabs was determined periodically for 28 days. The metabolic rate of the males remained essentially unchanged through day 3. By day 7, however, the metabolic rate had dropped to 32% of that of untreated crabs; by day 21 the rate had decreased by 48%; and by day 28 the rate was 20% lower than the base-line value. In the female, oxygen uptake values also decreased by day 7, but by day 14 the metabolic rate returned to the base-line rate and remained essentially at this level through day 28. Although initially the same, the rate of oxygen uptake of males was significantly lower than that of the females after 21 days in this sublethal concentration of mercury, and the metabolic rate of the males had not returned to the same level as it was before the crabs were placed in mercury by the end of the 28 day experimental period (Figure 4). Both males and females, however, continued to survive for another month under the same mercury regime as before without any significant increase in mortality.

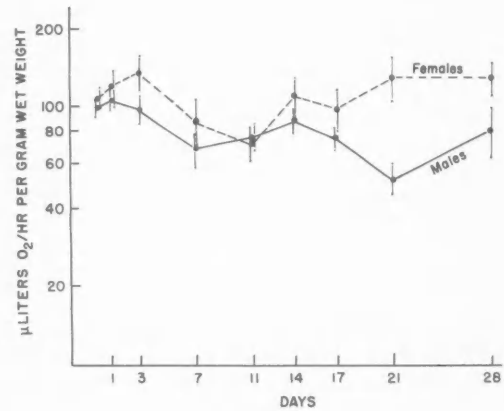

FIGURE 4.—Oxygen uptake rates of male and female *Uca pugilator* maintained in 30‰ seawater containing 9×10^{-7} M $HgCl_2$ (0.18 ppm) at 25°C. The base-line rate is represented by the first set of data points on the left. The vertical bar through each mean value is the standard error.

Under conditions of low temperature (5°C) and salinity (5‰) stress, not only did females survive much longer than males, but also the females were better able to maintain a steadier rate of oxygen uptake (Figure 5). The metabolic rate and pattern of the experimental female crabs were similar to those of the control female crabs. The metabolic rate of male experimental crabs was not significantly different from that of the female experimental or male and female control crabs, after a 1-day exposure to mercury, but by day 3 the rate dropped markedly (Figure 5).

Oxygen uptake rates of female control crabs maintained in low-salinity water (5‰) and at high temperature (35°C) were relatively constant over a 28-day period and tended to be higher than that of control male crabs (Figure 6). The metabolic rates of experimental female crabs remained fairly constant for the first 7 days and then declined rapidly. The uptake rates of experimental male crabs declined steadily from day 1 and tended to be lower than those of the females throughout the remainder of the time period (Figure 6).

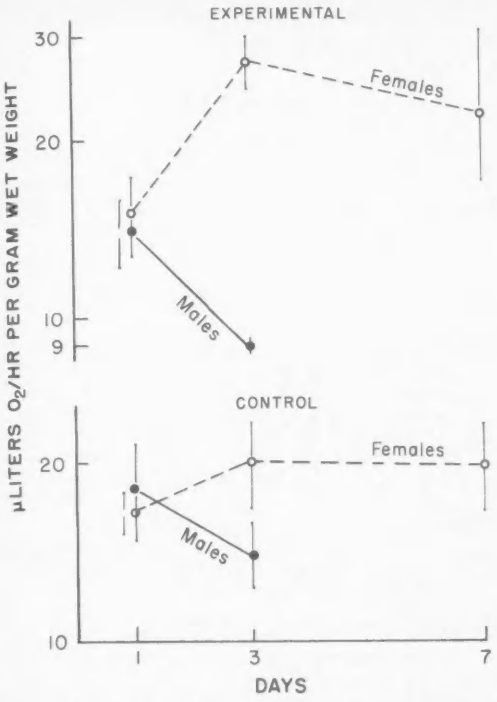

FIGURE 5.—Oxygen uptake rates of male and female *Uca pugilator* maintained at 5° in 5‰ seawater with and without the addition of 9×10^{-7} M $HgCl_2$ or 0.18 ppm. The vertical bar through each mean value is the standard error.

DISCUSSION

Fiddler crabs are capable of rapidly removing mercury from their surrounding aqueous media and retaining it in their tissues. However, not all tissues concentrate mercury to the same degree. The rapid accumulation and large concentration of mercury in gill tissue of fiddler crabs and the lesser but significant amounts of mercury found in the hepatopancreas and green gland are similar to results obtained in experiments involving other heavy metals. Bryan (1966), for example, found the highest concentration of zinc in the gills and hepatopancreas. He related these concentrations to the fact that excess zinc can be stored in the hepatopancreas in the crab *Carcinus maenus* and concentrated and excreted across the gills.

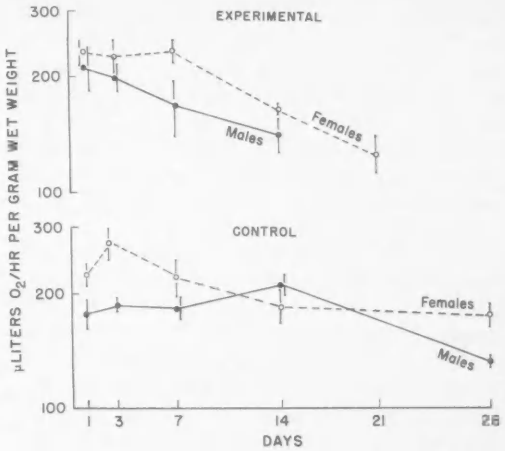

FIGURE 6.—Oxygen uptake rates of male and female *Uca pugilator* maintained at 35°C in 5‰ seawater with and without the addition of 9×10^{-7} M $HgCl_2$ or 0.18 ppm. The vertical bar through each mean value is the standard error.

Uca pugilator can adapt quickly to a wide range of adverse environmental fluctuations (Vernberg and Vernberg, 1970). The sudden changes in temperature and salinity that do occur usually do not persist for prolonged periods of time, and conditions usually ameliorate within a week or two. Results presented in this paper indicate that the crabs can withstand low salinity and high temperature better than low salinity coupled with low temperature, findings consistent with the earlier generality proposed by Panikkar (1940). Further, Lockwood (1962) stated that since ionic regulation is thermally influenced, organisms survive dilute medium more successfully when the rate of ion uptake as compared with ion loss increases faster with increasing temperature. Under both sets of conditions, however, the added stress of concentrations of mercury that are sublethal under optimum conditions adversely affected survival rates under stressful conditions and more markedly in males than in females. Bryan (1971) has speculated that the increased lethality of a heavy metal under stressful conditions is in some way related to changing rates of absorption. Our data are another example of the principle

that multiple environmental factors, each at a sublethal level, interact synergistically to cause death. Earlier papers, especially the classic paper of McLeese (1956), emphasized the lethal role of "normal" environmental factors, whereas we have demonstrated the importance of pollutants as part of the "normal" environment of many species.

Under optimal conditions of temperature and salinity mercury generally decreased metabolic rates of the males; effect on metabolic rates of females was much less pronounced. This differential effect of mercury on the metabolism of males and females is difficult to understand. On an interspecific basis, differences between resistance of larvae of *Artemia salina* and *Elminius modestus* to mercury have been related to differences between rates of uptake rather than of tissue resistance (Corner and Rigler, 1958). However, since the amount of mercury in tissues of both male and female fiddler crabs was essentially the same, these differences would not appear to be related to differences in uptake of the mercury. Under conditions of thermal and salinity stress without the addition of mercury the metabolic rate of the female crabs tended to be more stable and less depressed than the rate of male crabs. The addition of mercury to the already stressful conditions accentuated these differences.

Our results indicate, then, that a concentration of mercury that is sublethal under optimum conditions of temperature and salinity, may greatly reduce the ability of the population to survive under normally stressful conditions of temperature and salinity flux.

ACKNOWLEDGMENTS

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LENGTH-WEIGHT RELATIONSHIP, FOOD HABITS, PARASITES, AND SEX AND AGE DETERMINATION OF THE RATFISH, *HYDROLAGUS COLLIEI* (LAY AND BENNETT)[1]

ALLYN G. JOHNSON[2] AND HOWARD F. HORTON[3]

ABSTRACT

In the fall and winter of 1965-1967, 292 ratfish (*Hydrolagus colliei*) were collected from four locations off the Pacific coast of Oregon. Specimens were examined for length-weight relationships, food habits, parasites, and a method of sex and age determination. Equations describing the body weight-body length (snout to vent) relationships were log weight = log −4.3217 + 3.0546 log length for males, and log weight = log −4.1692 + 2.9720 log length for females. The food organisms most important to ratfish were shrimp (*Pandalus* and *Crago*), mollusks (*Musculus* and *Amphissa*), and echinoderms (*Brisaster*). Two occurrences of cannibalism were found in ratfish collected off Cape Arago, Oreg. Infestations by *Gyrocotyle* ranged from 29 to 66% among samples from the four locations. The copepod, *Acanthochondria* sp., was attached to the claspers of seven males from Cape Arago. Eye-lens weights (wet and dry), vertebral radii, basal sections of the dorsal spine and left pectoral fin, and body-length frequencies were studied, but no accurate method of age determination was found. Tritors on the posterior side of the vomerine dental plate may be indicative of age, but the precise relationship was not determined.

The ratfish, *Hydrolagus colliei* (Lay and Bennett), is a member of the class Chondrichthyes, order Chamaeriformes, and family Chimaeridae (Bailey, 1970). Distributed from western Alaska to northern Baja California (Koratha, 1960), this cartilaginous fish is the only chimaeroid found on the Pacific coast of Canada and the United States. Ratfish are of little economic value, but their liver oil is an excellent lubricant and could be used commercially (Clemens and Wilby, 1961). Ratfish are an important source of food for such commercial fishes as soupfin sharks, *Galeorhinus zyopterus* (Nakatsu, 1957), spiny dogfish, *Squalus acanthias* (Alverson and Stansby, 1963), and Pacific halibut, *Hippoglossus stenolepis* (Thompson, 1915). Conversely, ratfish are commonly caught in the trawls of commercial fishermen who consider them a nuisance. Our study was conducted to help fill the need for more information on the general biology of this primitive fish (Bigelow and Schroeder, 1953; Crescitelli, 1969).

Little information has been published on the food habits of *H. colliei*. Dean (1906) reported that *Chimaera* (*Hydrolagus*) *colliei* fed on small isospondylous fishes, opisthobranchs, annelids, crustaceans, mollusks, squids, and nudibranchs. Olsson (1896) and Legendre (1944) reported that *Chimaera monstrosa* fed on mollusks, decopods, annelids, amphipods, echinoderms, and coelenterates.

Several studies have been conducted on the parasites of *H. colliei*. Wardle (1932) reported that most ratfish contained a pair of *Gyrocotyle urna* in the anterior region (spiral valve) of the intestine. Lynch (1945) concluded that *G. urna* should be divided into *G. urna* and *G. fimbriata*. Koratha (1960) examined two *H. colliei* from

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Baja California and found two digenea (*Otodistomum* sp.) and one cestode from the intestine, one hirudinean (*Branchellion* sp.) from the skin surface, and three copepods (*Chondracanthus epacthes*) and one monogenea from the gills. A monogenea reported from the gills of ratfish from Washington waters was *Octobathrium leptogaster* (Bonham, 1950). Wilson (1935) reported the copepods *Acanthochondria clavata* and *A. epachthes* from the claspers and gills, respectively, of *H. colliei* from California waters. Kabata (1968) could not accept Wilson's (1935) identification of *A. clavata*, because the species had never been found outside the North Sea, and described *A. holocephalarum* from the claspers of ratfish captured off British Columbia.

Most morphometric studies of ratfish have been descriptive or histological in nature. Sanford, Clegg, and Bonham (1945) studied the liver oil and vitamin A content of 35 ratfish captured off Tatoosh Island, Wash. These factors were related later to size and sex of ratfish by Pidlaoan (1950). Halstead and Bunker (1952) described the venom apparatus and anatomy of the dorsal spine of ratfish. They concluded that the venom of *H. colliei* was not capable of inflicting fatal injuries to man. A histological study of the digestive tract and of the pituitary of *H. colliei* was conducted by Clothier (1957) and Sathyanesan (1965), respectively.

Stanley (1961) performed a morphometric study of the genital systems of *H. colliei* and found that summer was the peak reproductive period although one-third of the females and all of the males evidenced reproductive activity throughout the year. Sexual maturity was attained at 24-25 cm (S-V)[4] for females and 18.5-20 cm (S-V) for males.

METHODS

Four collections totaling 292 ratfish were made by otter trawl off the coast of Oregon at depths ranging from 50 to 120 fm from 1965 to 1967. The collection from off Newport ($N = 189$) was frozen while specimens collected off Cape Blanco ($N = 44$), Cape Arago ($N = 35$), and Astoria ($N = 24$) were preserved in 10% Formalin.

All ratfish were examined as follows: Sex was determined by inspection of the gonads; snout to vent length was measured in millimeters, and total weight was measured in grams; all specimens were examined for internal and external parasites; alimentary canals were examined along their entire length for food items; and dental plates, dorsal spines, left pectoral fins, and a piece of the vertebral column were decalcified, sectioned frozen, treated with Delafield's hematoxylin stain, and examined for growth structures indicative of age. Both eye lenses were removed from specimens in the Newport and Astoria collections. The wet and dry weight of each lens was determined to the nearest ten thousandth of a gram. For wet-weight determinations, lenses were stored in 10% Formalin for 1 month, removed and blotted, and immediately weighed. For dry weight determinations, the lenses were then desiccated at 80°C for 82 hr and reweighed. The 82-hr drying period was determined from a curve of weights of 10 lenses dried at 80°C and weighed at progressive time intervals. The 82-hr period assured evaporation to a stable weight.

Most statistical analyses of body length-body weight and body length-eye-lens weight relationships were performed on a CDC 3300 computer[5] utilizing program FISH 6669 in the Department at Oregon State University.

RESULTS AND DISCUSSION

There was a highly significant correlation ($P = 0.01$) of body length to body weight for male and female ratfish in the large Newport collection and for the aggregate of each sex collected (Table 1). Based on the coefficient of determination (r^2) (Croxton, 1953), more than 87% of the variation in weight in males and more than 96% in females was attributable to the variation in length of the ratfish. The length-

[4] Body length measured from the tip of the snout to the anterior edge of the vent.

[5] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

TABLE 1.—Data to describe length-weight relationship (log weight = log a + b log length) for male and female ratfish collected off Oregon during 1965-67.

Location	Sex	Sample size	Constant log a	Constant b	r	Sign. Level of r (P = 0.01)*	r^{2**}
Newport	Male	128	−2.0168	2.0447	0.9352	0.234	0.8746
Newport	Female	56	−3.1384	2.5336	.9824	.361	.9651
Total†	Male	175	−4.3217	3.0546	.9917	.210	.9835
Total†	Female	112	−9.1692	2.9720	.9943	.257	.9886

* From Table X in Quenouille (1952).
** Coefficient of determination (Croxton, 1953).
† Composite of collections from Newport, Astoria, Cape Arago, and Cape Blanco.

weight relationship for male and female ratfish collected off Newport is defined and illustrated in Figure 1.

A taxonomic list of all food organisms identified from the alimentary canals of 283 ratfish is presented in Table 2. The table also contains lists of the relative importance of food items by the frequency of occurrence and numerical methods (Lagler, 1956) and gives the locations of the collections in which the food items were found.

Based on these data, ratfish appear to be opportunistic feeders. The most important food items (>10% occurrence) were shrimp (*Pandalus* and *Crago*), mollusks (*Musculus* and *Amphissa*), and echinoderms (*Brisaster*). In general, young and adult ratfish ate the same foods. Dean (1906) found seaweed in the alimentary canals of ratfish, but we did not find any plant materials in the specimens we examined.

In the Cape Arago collection, ratfish were eaten by ratfish. One egg capsule and a caudal fin were eaten by two large females (280 mm). We are not aware of any previous record of cannibalism in ratfish. Of the teleostomi, flatfish appeared to be taken most frequently by ratfish. The two flatfish found were *Hippoglossoides elassodon* and *Esopsetta jordani*.

In the food habits study, we did not use a volumetric method of examination because in many alimentary canals only shells and fragments remained. Also, materials such as carapaces of shrimp have a large surface to volume relationship which causes them to displace little water or to float. Ratfish often void ingested matter between capture and landing, making volumetric measurements inaccurate. Dean (1906) commented on this habit, and we noticed it in ratfish captured by hook and line. In addition, we found *Gyrocotyle* in the mouths of some trawl-caught ratfish, indicating that the contents of the alimentary canals recently had been voided. According to Lynch (1945), *Gyrocotyle* would normally be restricted to the anterior section of the intestine (spiral valve).

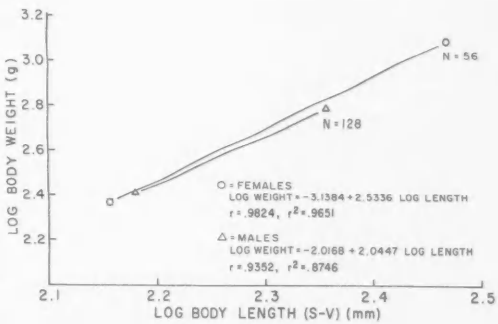

FIGURE 1.—Length-weight relationship of male and female ratfish collected off Newport, Oreg., 1965.

The parasites found on or in the ratfish were *Gyrocotyle urna*, *G. fimbriata*, and the copepod, *Acanthochondria* sp. Table 3 lists the frequency of *Gyrocotyle* occurring in the four collections of ratfish. Both *G. fimbriata* and *G. urna* appeared in about equal numbers in the Newport collection, but only *G. fimbriata* occurred in the Astoria and Cape Arago collections. The frequency of infestation by *Gyrocotyle* in young fish from the Cape Blanco collection was 30%. We did not find evidence of mass infestation by *Gyrocotyle*, as suggested by Wardle (1932). The young fish (<50 mm) contained from zero to two *Gyrocotyle* each. The voiding of canal contents by the ratfish interfered with obtaining an accurate estimation of the degree of infestation.

TABLE 2.—Taxonomic list[1] and relative importance of food organisms identified from the alimentary canals of 283 ratfish (*Hydrolagus colliei*)[2] collected off Oregon during 1965-1967.

Organisms	Frequency of occurrence (%)	Numerical method[3]		Location[4]			
		Organisms	%	A	N	CA	CB
Phylum Annelida							
Class Polychaeta							
Aphrodita	4.4	10	1.0	x	x		x
Unidentified	2.2	10	1.0		x		x
Phylum Mollusca							
Class Gastropoda							
Amphissa	33.4	1,016	74.5	x	x	x	x
Amygdalum	2.2	9	1.0				x
Yoldia	2.6	6	0.0+		x		
Musculus	24.6	66	4.9	x	x	x	x
Leptopecten	0.9	2	0.0+		x		
Pecten	1.8	7	0.0+			x	
Cardiomya	6.1	27	2.0				x
Calliostoma	0.4	1	0.0+				x
Searlesia	0.4	1	0.0+	x			
Class Scaphopoda							
Dentalium	3.1	7	0.0+		x		x
Phylum Arthropoda							
Class Crustacea							
Livoneca	4.8	26	2.0		x	x	x
Crago	12.3	32	2.3		x		
Pandalus	20.2	81	5.9	x		x	x
Cancer	0.9	2	0.0+	x	x		
Chionoectes	0.4	1	0.0+				x
Unidentified	3.5	13	1.0		x		
Phylum Echinodermata							
Class Echinoidea							
Brisaster	11.0	25	1.8	x	x	x	
Strongylocentrotus	0.9	2	0.0+	x		x	
Phylum Chordata							
Class Chondrichthes							
Hydrolagus	0.9	2	0.0+			x	
Class Osteichthyes							
Pleuronectidae	0.7	2	0.0+		x	x	
Unidentified	5.5	13	1.0	x	x	x	
Unknown	0.4	1	0.0+		x		
Total		1,362	98.4+				

[1] After Smith et al. (1954), Barnes (1963), and Bailey (1970).
[2] Of the 283 ratfish, 224 contained food organisms.
[3] Fragments (less than one-half an animal) were recorded as one individual.
[4] Locations were: A = Astoria, N = Newport, CA = Cape Arago, and CB = Cape Blanco.

Gyrocotyle were found lodged in the folds of the spiral valve and were not embedded in the intestinal wall, thus making expulsion by violent intestinal movements possible.

In the Cape Arago collection, 7 of the 21 adult male ratfish had from two to eight *Acanthochondria* sp. attached to the free ends of their claspers. The immature males and the females did not carry this copepod. The species is similar to, but not the same as, *A. compacta*.[5]

An unidentified fungus, which occurred on the intestine of 29% of the Newport collection, was not necessarily a parasite as it may have developed in the interval between capture and preservation. No visible lesions or other damage were noticed on the body or alimentary canal surfaces of the ratfish in which the fungus occurred. The fungus appeared to be of nonseptate, white, filamentous type.

Sex and relative age of ratfish can be determined by examination of the secondary sex characteristics. Males possess a frontal tenaculum, prepelvic tenacula, and claspers, whereas fe-

[5] Personal communication, Dr. Satyu Yamaguti, Beltsville, Md., June 13, 1967.

TABLE 3.—*Gyrocotyle* found in 283 ratfish (*Hydrolagus colliei*) collected off the coast of Oregon, 1965-1967.

Location	Total number of *Gyrocotyle*[1]			Number of ratfish examined	Percent infested[2]
	G. fimbriata	*G. urna*	Unidentified		
Newport	50(34)	62(39)	38(25)	184	53.2(60.0)
Astoria	8(7)	-- --	-- --	24	29.2(31.8)
Cape Arago	40(23)	-- --	-- --	35	65.8(79.4)
Cape Blanco	18(11)	4(2)	-- --	40	30.0(35.4)

[1] Number in parenthesis is the number of ratfish infested.
[2] Number in parenthesis is the percent infestation when alimentary canals that contained neither food nor parasites were excluded.

males do not possess these structures but develop paired oviducal openings not possessed by males. Development of these structures can be used to separate ratfish into young, immature, and adult age groups. Young males have a frontal tenaculum streak and diminutive claspers (Figure 2); immature males have a small frontal tenaculum and claspers which are not perforated at their free ends (Figure 3); and mature males have a well-developed frontal tenaculum and well-developed claspers which are perforated at their free ends (Figure 4). Young females have no oviducal openings (Figure 2); the oviducts of immature females have small openings (Figure 3); and mature females have oviductal openings which are large, elongated, and swollen

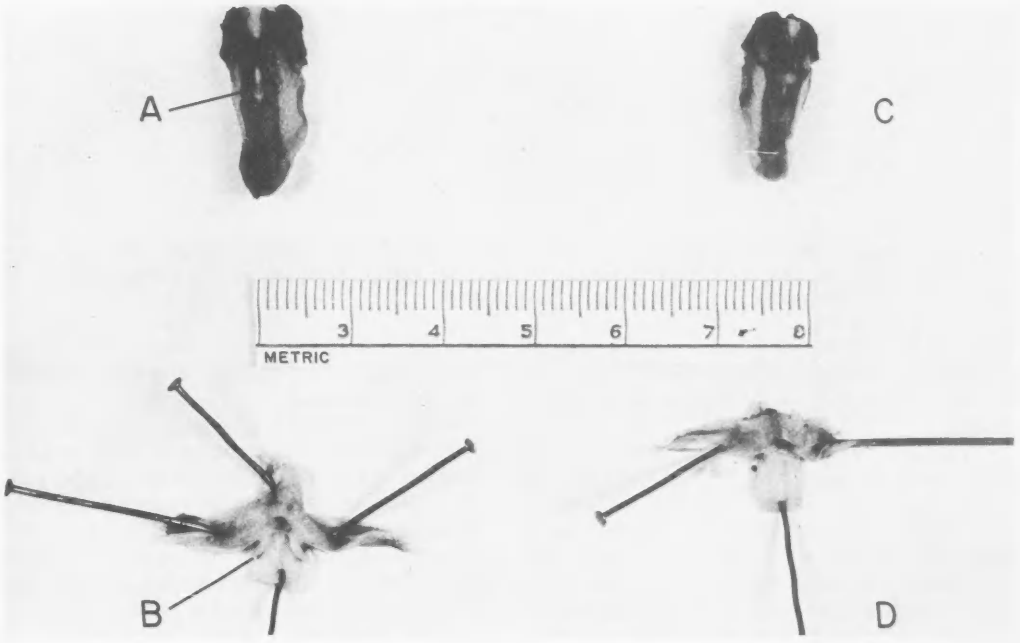

FIGURE 2.—Regions of young ratfish showing (A) the frontal tenaculum streak, and (B) the small claspers of the male; and (C) the absence of a frontal tenaculum streak, and (D) the absence of oviductal openings in the female.

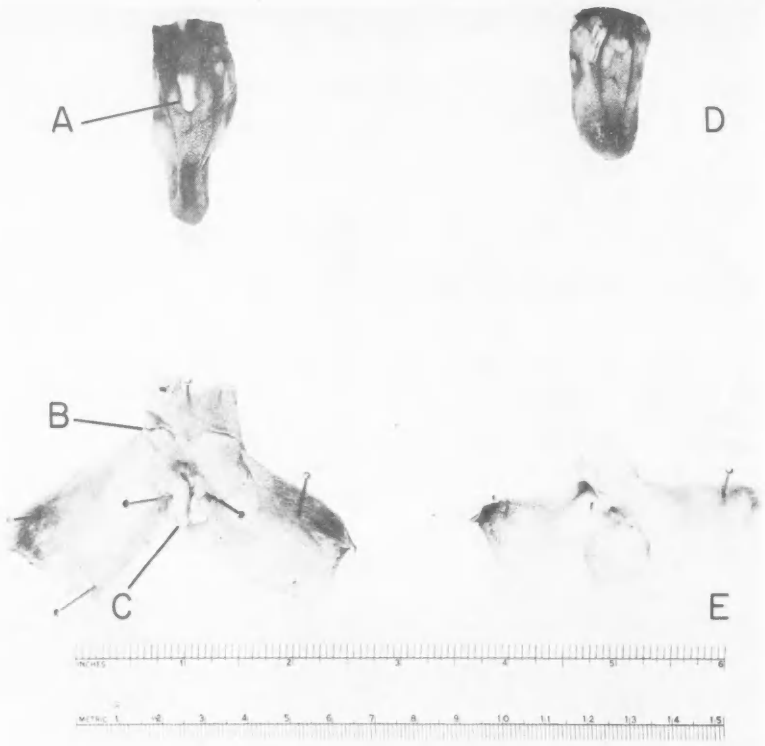

FIGURE 3.—Regions of immature ratfish showing (A) the frontal tenaculum, (B) the prepelvic tenacula, and (C) the claspers of the male; and (D) the absence of a frontal tenaculum, and (E) the presence of small openings to the oviducts of the female.

(Figure 4). Attempts to age ratfish on the basis of length-frequency distributions were inconclusive.

When dry eye-lens weight was compared to body length for specimens in the Newport collection, lens weight was positively correlated with increasing body length for males (N = 128), but was not correlated with body length for females (N = 56) (Figure 5). There was no difference in the dry weights of the right and left eye lens at the 95% level of confidence. Wet eye-lens weights were similarly related to body lengths with the coefficient of determination (r^2) for males being 0.8788 and 0.9292 for the right and left eye lens respectively, and for females being 0.0017 and 0.0133 for the right and left eye lens respectively.

We can offer no logical explanation for the lack of positive correlation between eye-lens weight and body length for female ratfish. Data for males and females were processed simultaneously and were consistent, by sex, for left and right and for wet and dry eye-lens weights. Because all but eight females exceeded 230 mm in length, most eye-lens growth may take place between birth (30-40 mm [Stanley, 1961]) and maturity (240-250 mm [Stanley, 1961]). The possibility of decreasing density of the lens with size (and maturity) should be investigated.

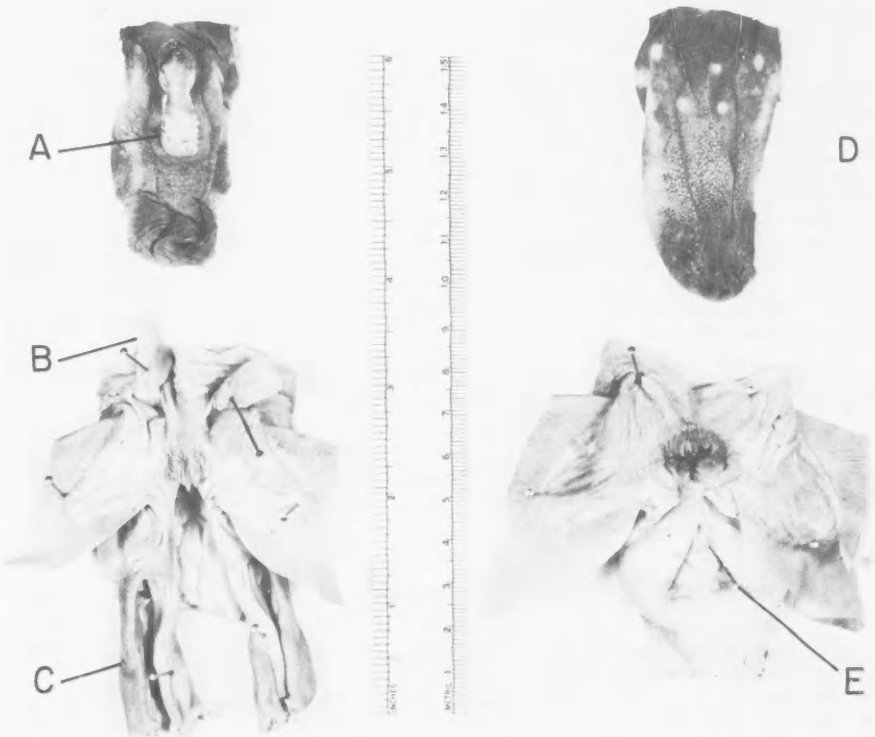

FIGURE 4.—Regions of mature ratfish showing (A) the frontal tenaculum, (B) the prepelvic tenacula, and (C) the claspers of the male; and (D) the absence of a frontal tenaculum, and (E) the presence of well-developed openings to the oviducts of the female.

In general, there was an increase in the size of other body parts (teeth, vertebrae, base of left pectoral fin, and base of dorsal spine) with increasing body length. We did not find any layering or structures in these body parts which were sufficiently correlated with body length to provide a possible means of age determination.

The number of tritors (horizontal ridges) on the posterior side of the left vomerine dental plate was compared to the respective body length of male and female ratfish in the Cape Blanco and Newport collections. In general, the number of tritors increased with increasing body length (Figure 6). Two problems arose in using this structure as a basis for age determination: (1) No comparison to known-aged fish was possible. (2) The amount of wear on these ridges per unit of time was not known.

ACKNOWLEDGMENTS

Drs. C. E. Bond, R. E. Millemann, R. C. Simon, and J. D. Hall, Department of Fisheries and Wildlife, Oregon State University, provided counsel and reviewed the manuscript. Dr. W. S. Overton, Department of Statistics, Oregon State University, provided direction in the statistical analyses. Special thanks are due personnel of the Fish Commission of Oregon for assistance in obtaining ratfish for this study. James Meehan and Gary Milburn were particularly helpful.

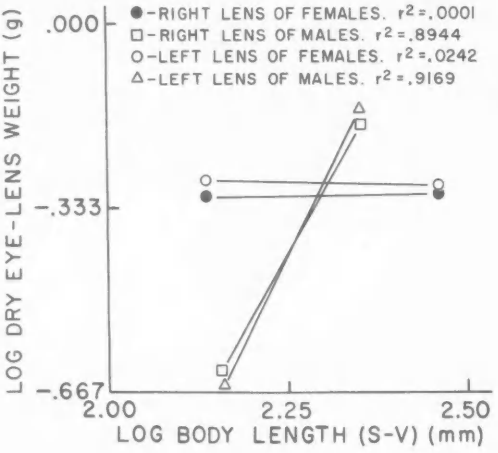

FIGURE 5.—Log dry eye-lens weight compared to log body length for ratfish collected off Newport, Oreg., 1965.

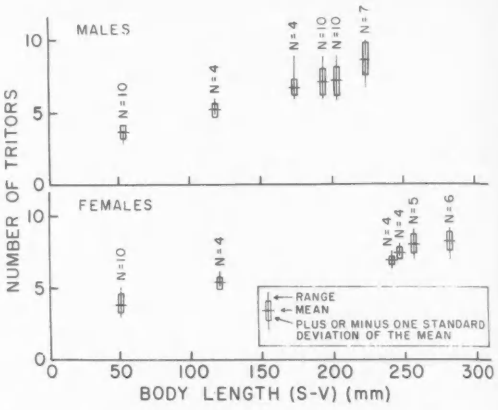

FIGURE 6.—Comparison of the number of tritors on the posterior side of the vomerine dental plate to body length of ratfish collected off Oregon, 1965-1967.

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OCEAN DISTRIBUTION, GROWTH, AND EFFECTS OF THE TROLL FISHERY ON YIELD OF FALL CHINOOK SALMON FROM COLUMBIA RIVER HATCHERIES

KENNETH A. HENRY[1]

ABSTRACT

Data are presented depicting the distribution of some stocks of Columbia River hatchery fall chinook salmon in the northeast Pacific Ocean. These are based on recoveries of marked fish. Also presented are the apparent growth histories for fish from the Kalama and Spring Creek Hatcheries as well as a graphic population model for Columbia River fall chinook salmon. Finally, the effect on total yield for varying troll fishing mortalities for the 3-, 4-, and 5-year-old fish is analyzed and the results depicted in three-dimensional yield diagrams. In most instances, at least at the lower levels of estimated natural mortality, troll fishing of the younger fish reduced total yield.

A cooperative program was undertaken between the various fishery agencies in the United States and Canada to estimate the contributions to various fisheries of fall chinook salmon (*Oncorhynchus tshawytscha*) produced by a number of Columbia River hatcheries. Approximately 10% of the output from 12 hatcheries for the brood years 1961-64 was marked by the removal of certain fins. The design of this experiment, including a detailed account of the procedures used in calculating the number of marked fish recovered, and details of mark recoveries for the 1961 brood have been reported by Worlund, Wahle, and Zimmer (1969). Details of mark recoveries for the 1962 and 1963 broods were given by Rose and Arp (1970)[2] and by Arp et al. (1970[3], respectively. Cleaver (1969) made a detailed analysis of the 1961 brood based on mark recoveries. His analysis included estimating ocean mortality rates, maturity schedules, and, for the Spring Creek and Kalama fish, the effect of no ocean fishing on total yield. Henry (1971) made a similar analysis for the 1962 brood and, wherever possible, compared the results with those obtained for the 1961 brood. The general release and recovery areas covered by this marking program are shown in Figure 1.

Although a total of 12 hatcheries was involved in this study, fish from only two hatcheries, Spring Creek and Kalama, received specific identifying marks for all 4 years. Each year fish from two of the other ten participating hatcheries (but two different ones each year) also received special identifying marks. In addition to specific marks for four hatcheries each year, a certain proportion of the output from all participating hatcheries had a common mark. This mark — that is a composite of all the hatcheries — is referred to as the general mark. Thus, it is possible for only Spring Creek, Kalama, and general mark fish to analyze mark recoveries from all four brood years.

In the report, I have analyzed the mark recoveries for Spring Creek, Kalama River, and general marked Columbia River hatchery fall chinook salmon from the four consecutive brood

[1] National Marine Fisheries Service Northwest Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98102.

[2] Rose, J. H., and A. H. Arp. 1970. Contribution of Columbia River hatcheries to harvest of 1962 brood fall chinook salmon (*Oncorhynchus tshawytscha*). Bur. Commer. Fish., Columbia Fish. Program Off., Appraisal Section, Portland, Oreg. 27 p. (processed).

[3] Arp, A. H., J. H. Rose, and S. K. Olhausen. 1970. Contribution of Columbia River hatcheries to harvest of 1962 brood fall chinook salmon (*Oncorhynchus tshawytscha*). U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Columbia Fish. Program Off., Portland, Oreg., Econ. Feasibility Rep. 1. 33 p. (processed).

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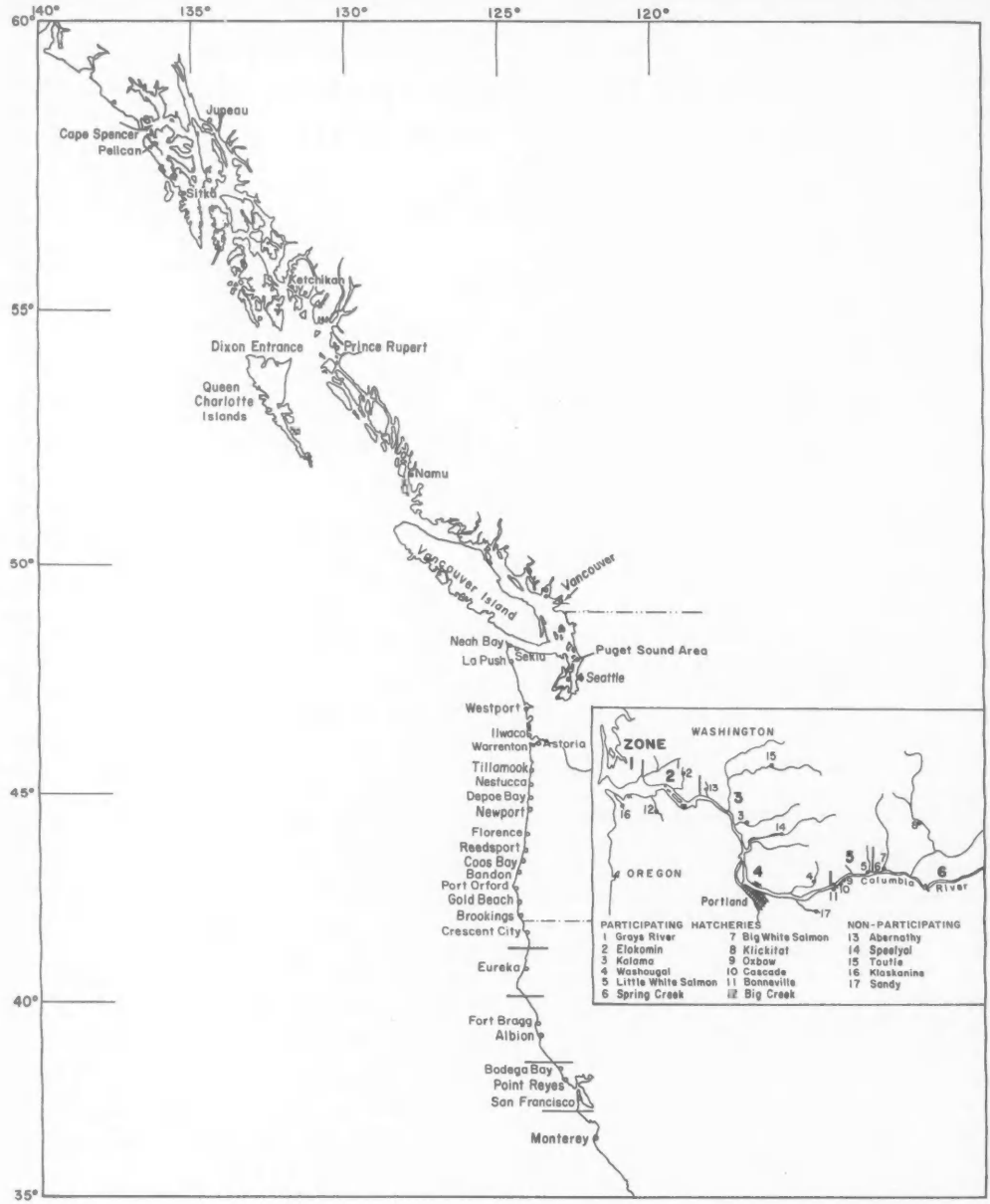

FIGURE 1.—Sampling areas in marine fisheries and release locations (inset) for the Columbia River hatchery evaluation program (from Lander, 1970).

years (1961, 1962, 1963, and 1964). I have demonstrated some of the differences in ocean distribution, contributions to various fisheries, and growth that occur between hatcheries—even within hatcheries—for different brood years. I also have presented a graphic population model for Columbia River fall chinook salmon. This model depicts all the factors affecting these stocks of salmon throughout their life history. Finally, within the general framework of the mortality estimates developed for the 1961 brood (Cleaver, 1969) and 1962 brood (Henry, 1971), I have analyzed the portion of the population model pertaining to the commercial fisheries to determine the overall effect on total yield for varying levels of ocean troll fishing mortalities on the 3-, 4-, and 5-year old fish.

RECOVERIES BY AREA

The ocean distribution of mark recoveries and contributions to the various fisheries was quite different for Kalama, Spring Creek, and general marked fish. Pulford (1970) listed the contribution of Columbia river hatchery fall chinook (all hatcheries combined) to the various fisheries along the Pacific Coast for 1966 only. Lander (1970) analyzed the distribution along the coast and contribution to the various fisheries in considerable detail for each hatchery; his data included sampling through 1966 only. In Table 1 are listed the calculated total recoveries by geographical area for the 1961 through 1964 brood years of special marked Kalama and Spring Creek fall chinook salmon and general marked

TABLE 1.—Calculated total recoveries, by age of fish and type of mark, for fall chinook salmon of the 1961-64 broods that were marked and released at Columbia River hatcheries.

Brood and area	Spring Creek mark age (years)					Kalama mark age (years)					General mark age (years)				
	2	3	4	5	Total	2	3	4	5	Total	2	3	4	5	Total
1961															
Alaska	*	0	0	0	0	*	5	35	4	44	*	0	7	0	7
Brit. Col.	*	841	164	5	1,010	*	441	480	91	1,012	*	4,106	1,871	218	6,195
Wash. Com.	4	1,084	82	0	1,170	0	149	142	7	298	0	3,241	455	41	3,737
Wash. Sport	152	431	97	0	680	21	78	100	9	208	375	1,681	416	67	2,539
Oreg. Ocean	4	130	24	0	158	0	21	4	0	25	0	396	36	0	432
Col. River	22	518	685	17	1,242	0	38	399	111	548	72	2,158	3,544	176	5,950
Calif.	*	25	0	0	25	*	2	0	0	2	*	23	0	6	29
Total	182	3,029	1,052	22	4,285	21	734	1,160	222	2,137	447	11,605	6,329	508	18,889
1962															
Alaska	0	0	0	0	0	0	0	4	0	4	0	0	5	2	7
Brit. Col.	0	75	90	9	174	0	162	155	23	340	51	1,183	802	48	2,084
Wash. Com.	0	150	33	5	188	0	47	15	0	62	8	973	130	4	1,115
Wash. Sport	34	140	24	0	198	0	76	7	8	91	163	540	108	27	838
Oreg. Ocean	0	11	3	0	14	0	8	4	0	12	2	37	3	0	42
Col. River	10	272	85	0	367	6	21	60	10	97	50	1,216	606	24	1,896
Calif.	0	0	0	0	0	0	0	0	0	0	0	6	0	0	6
Total	44	648	235	14	941	6	314	245	41	606	274	3,955	1,654	105	5,988
1963															
Alaska	0	0	0	0	0	0	5	14	0	19	0	0	9	*	9
Brit. Col.	23	557	224	6	810	0	233	195	45	473	55	4,464	2,246	201	6,966
Wash. Com.	0	381	38	0	419	0	107	71	5	183	5	3,227	464	10	3,706
Wash. Sport	120	329	103	0	552	138	139	53	12	342	1,189	2,569	451	46	4,255
Oreg. Ocean	0	63	10	0	73	2	27	13	0	42	4	652	165	3	824
Col. River	29	164	275	15	483	7	32	44	47	130	121	1,182	2,418	317	4,038
Calif.	0	4	0	0	4	0	0	0	0	0	0	12	12	15	39
Total	172	1,498	650	21	2,341	147	543	390	109	1,189	1,374	12,106	5,765	592	19,837
1964															
Alaska	0	0	*	*	0	0	0	*	*	0	0	0	*	*	0
Brit. Col.	7	589	432	16	1,044	0	45	478	64	587	10	1,339	1,446	92	2,887
Wash. Com.	0	906	127	0	1,033	0	65	37	5	107	4	2,268	354	3	2,181
Wash. Sport	244	581	70	10	905	38	44	26	0	108	483	1,506	249	0	2,212
Oreg. Ocean	127	171	27	0	325	0	10	13	0	23	151	614	170	0	935
Col. River	15	447	504	24	990	0	3	58	56	117	19	1,001	1,204	169	2,393
Calif.	0	8	2	0	10	0	0	0	0	0	0	0	1	0	1
Total	393	2,702	1,162	50	4,307	38	176	612	125	951	667	6,728	3,424	266	11,085

* No sampling.

Columbia River fall chinook salmon. No single fin marks are included. These same data are depicted in Figures 2-4 for calculated numbers of marked fish recovered and in Figures 5-7 as percentages of the total number of marks recovered by each age group within each brood year.

More Spring Creek mark recoveries (Figure 2) were recovered as age 3 fish than at any other age. Both the age 2 and age 3 recoveries came principally from Washington State fisheries, whereas most of the age 4 and age 5 recoveries were from the British Columbia troll fishery and the Columbia River gillnet fishery. For all ages combined, Washington State fisheries had the most recoveries of Spring Creek fish with about equal numbers recovered in the British Columbia and Columbia River fisheries. From 18 to 35% of the total recoveries were made in British Columbia fisheries (Figure 5). No Spring Creek fish were recovered from the Alaska fisheries.

The recoveries of marked Kalama fish were distributed somewhat differently than marked Spring Creek fish (Figure 3). Although recoveries of marked 2-year-old fish occurred primarily in the Washington sport fishery, 3- and 4-year-old recoveries and the recoveries for all ages combined came principally from the British Columbia troll fishery. Most of the recoveries occurred with the 3- and 4-year-old fish. British Columbia fisheries had from 40% to 60% of the total recoveries (Figure 6), a considerably higher percentage than for Spring Creek fish. There were very few recoveries from the Alaska fisheries.

General mark recoveries seemed to be more similar to Spring Creek recoveries than to Kalama recoveries, indicating that most of the fish from the participating hatcheries had an ocean distribution and maturity schedule more like Spring Creek fish than Kalama fish. For the general mark recoveries, the 2-year-old recoveries were mainly from the Washington sport fishery (Figure 4). The Washington fisheries accounted for 38-53% of the 3-year-old mark recoveries, whereas both the 4- and 5-year-old recoveries came mainly from the British Columbia troll fishery and the Columbia River gill-

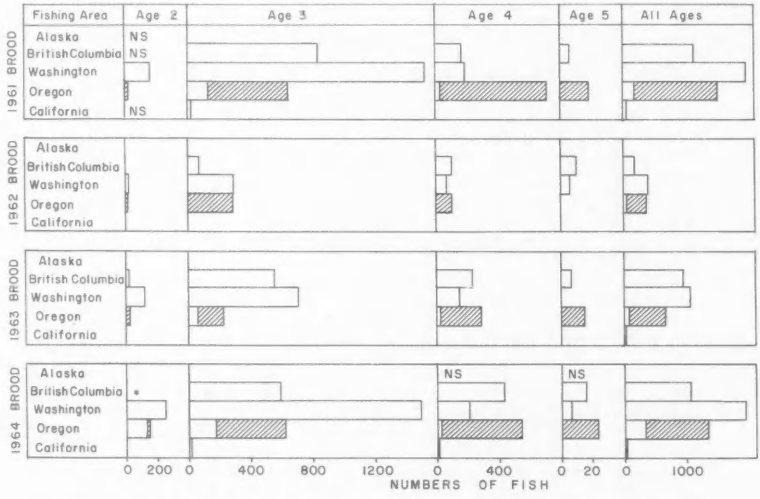

FIGURE 2.—Calculated total recoveries (in numbers of fish) of special marked Spring Creek hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 10 recoveries.

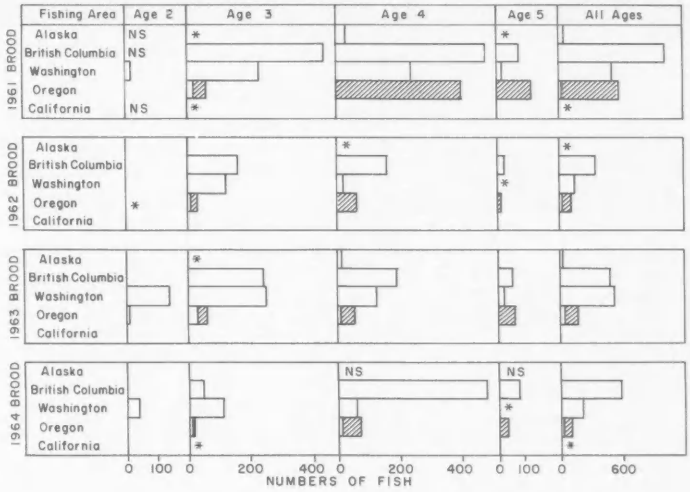

FIGURE 3.—Calculated total recoveries (in numbers of fish) of special marked Kalama hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 10 recoveries.

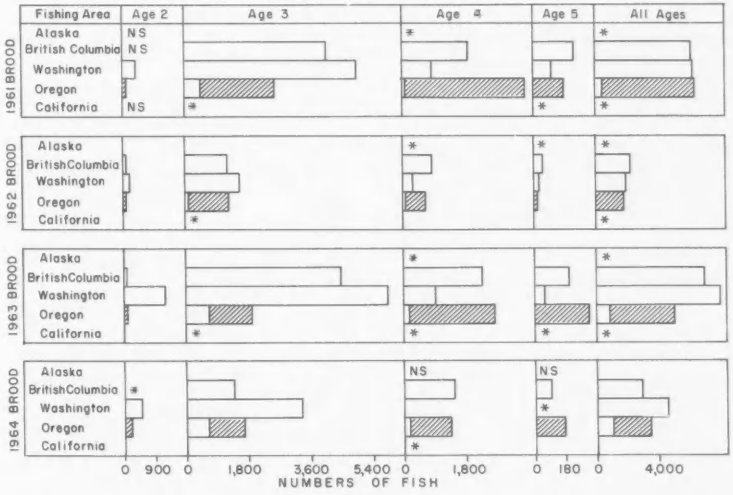

FIGURE 4.—Calculated total recoveries (in numbers of fish) of general marked Columbia River hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 50 recoveries.

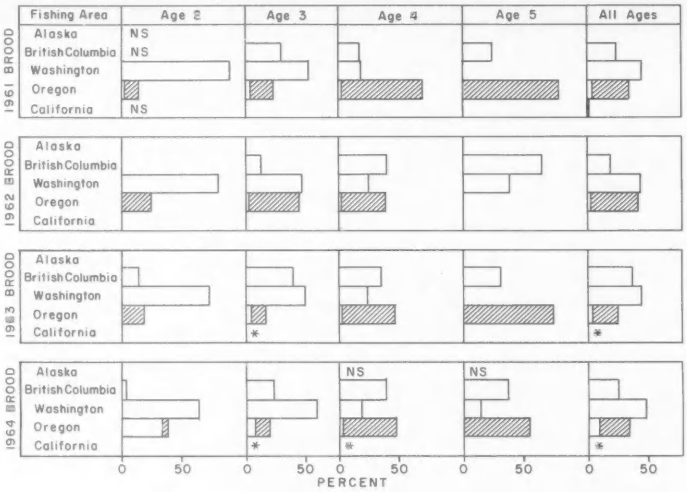

FIGURE 5.—Calculated total recoveries (in percent) of special marked Spring Creek hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 1 percent.

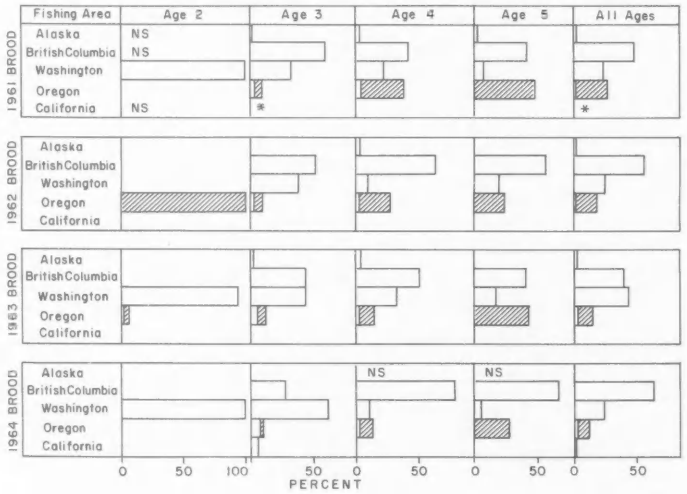

FIGURE 6.—Calculated total recoveries (in percent) of special marked Kalama hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 1 percent.

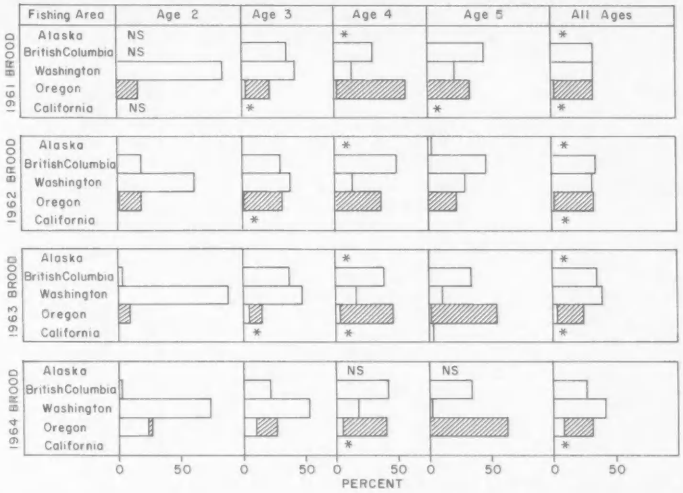

FIGURE 7.—Calculated total recoveries (in percent) of general marked Columbia River hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 1 percent.

net fishery (Figure 7). For all ages combined, the recoveries were fairly equally distributed between the British Columbia, Washington, and Columbia River fisheries.

As mentioned above, the age at recovery for Kalama fall chinook salmon was somewhat different than the age at recovery of the other two groups of marked fish. This is more clearly seen in Figure 8 where the calculated total ocean recovery of special marked Spring Creek, Kalama, and general marked fish (by age) for these four brood years is shown. Thus, for Spring Creek most of the ocean recoveries were as 3-year-old fish (66-83%); Kalama mainly as 3- (21-57%) and 4-year-olds (32-66%); and general marks mainly as 3-year-olds (64-73%).

SIZE AND GROWTH

Not only were the recoveries by age and area different for Spring Creek and Kalama fall chinooks, but these fish also experienced different apparent growth patterns. In Figure 9 are shown the average weights, by age and sex, of marked Spring Creek and Kalama fish recovered in the Columbia River gillnet fishery. The Kalama fall chinooks were generally smaller than the Spring Creek fish at ages 2-4, whereas the Kalama fish were larger at age 5. This change in the relative size of fish from these two stocks of salmon might reflect the selective effects of a more intensive troll fishery on the faster growing, earlier maturing Spring Creek fish, whereby the larger Spring Creek fish are more apt to be caught by the troll fishery at ages 2 and 3. Since data are limited for some of the sex-age categories, I have combined the data for all brood years and both sexes and have completed a von Bertalanffy type growth equation for these two stocks (Figure 10). The relatively faster growth at the younger ages and the more abrupt slowing down of growth at the older age is evident for the Spring Creek fish. Parameters calculated for Spring Creek were: $W_\infty = 12.76$ kg, $t_0 = 1.02$, and $k = 1.1$; for Kalama they were: $W_\infty = 18.44$ kg, $t_0 = 0.77$, and $k = 0.6$. These growth parameters clearly detail the growth differences between these two stocks and would be useful in any future dynamic pool type of analysis (Beverton and Holt, 1957) of potential production from them.

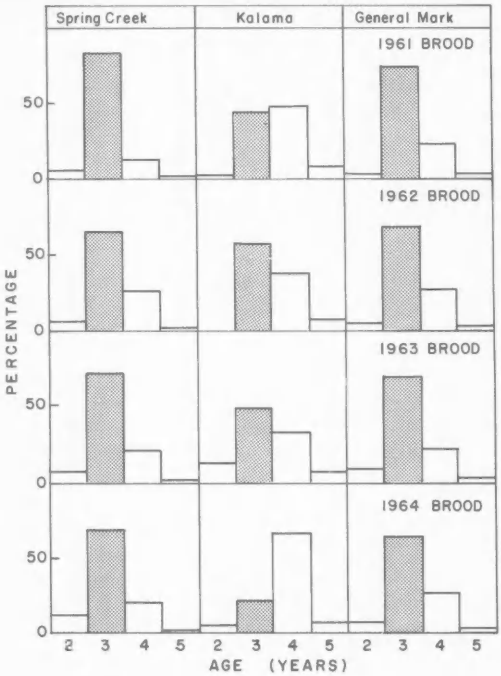

FIGURE 8.—Calculated total ocean recoveries (in percent), by age, of special marked Spring Creek, Kalama, and general marked Columbia River hatchery fall chinook salmon, 1961-64 brood years.

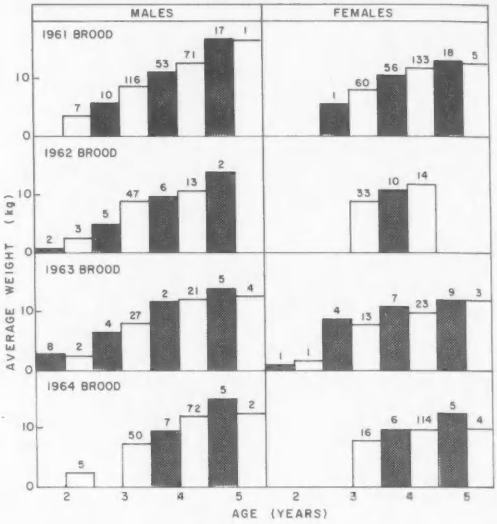

FIGURE 9.—Average weight (kilograms) by age and sex, of 1961-64 brood Spring Creek and Kalama special marked hatchery fall chinook salmon caught in the Columbia River gillnet fishery. Shaded columns represent data for Kalama salmon — clear columns, Spring Creek. Numbers indicate sample size.

GRAPHIC POPULATION MODEL FOR COLUMBIA RIVER FALL CHINOOK

To more clearly understand all the forces affecting a stock of fish, it often is convenient to depict the population in a simulated flow chart or block diagram. Shapiro and Andreev (1969) show such a diagram for chum salmon (*O. keta*). With some modification, their diagram also would be applicable to Columbia River fall chinook salmon as shown in Figure 11. This diagram is based on the following stock characteristics. There are five age groups, four of which are capable of entering the spawning groups, and each brood year diminishes in numbers as a result of natural mortality (M_i) and ocean fishing mortality (F_i). Ocean fishing mortality occurs only on the 2+, 3+, and 4+-year-old-fish. Growth and fecundity differ for each age group, and entry into the spawning part of the population is affected by a probability (P_i). The spawning group is diminished by a river fishing mortality (RF_i). After river fishing mortality, some portion of the spawning fish (k_i) are removed for artificial propagation. Survivals to recruitment resulting from artificial and natural reproduction are taken to be different. The number of recruits (R) is dependent on a survival relationship for the effective fecundity, i.e., R/E.

EFFECT OF TROLL FISHING ON YIELD

A complete analysis of the Columbia River fall chinook population, as depicted in Figure 11, is beyond the scope of this paper. However, I

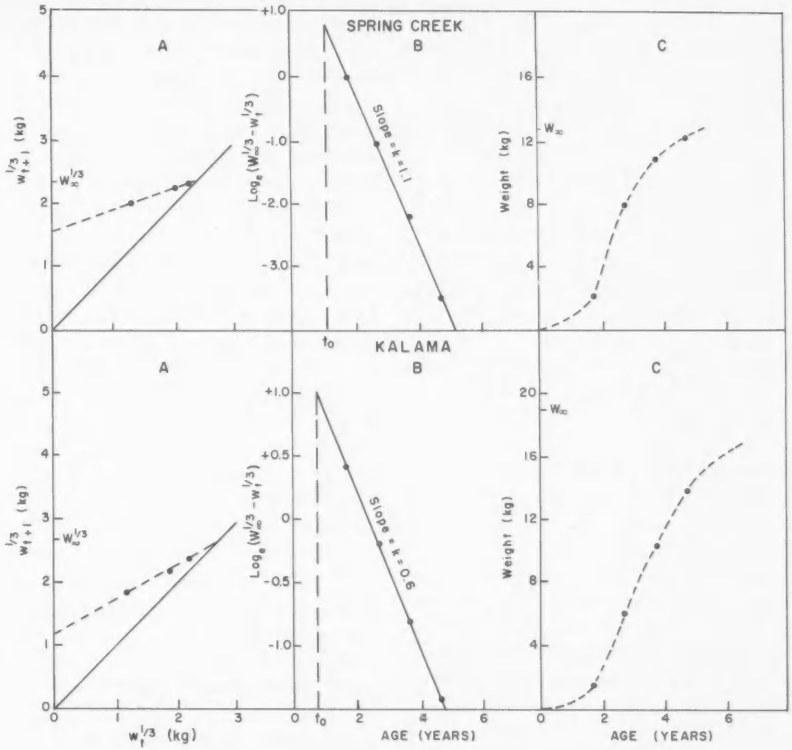

Figure 10.—Successive stages of fitting Spring Creek and Kalama Hatchery fall chinook salmon weight data from Figure 8 to the von Bertalanffy growth equation. Part A shows the relation between average weight at age t and age $t + 1$ — point on the dotted line where $w_t^{1/3} = w^{1/3}_{t+1}$ is an estimate of $W_\infty^{1/3}$. Part B shows the relation between age and a logarithmic function of the weight used to estimate the value of k (i.e., the slope). Part C shows the calculated growth curve based on the values computed from Parts A and B.

want to analyze a part of the model, the part dealing with the ocean and river fisheries, to show the calculated effect the troll fishery has on total yield for a particular brood year. In these analyses, I have used data developed for the 1961 and 1962 brood years for the Spring Creek and Kalama fall chinooks, based on studies by Cleaver (1969) and Henry (1971), respectively. Where there were some data missing for the 1962 brood Spring Creek fish, I used 1961 data. The starting point for the analyses is at age 1+ in Figure 11.

It is apparent from Figure 11 that given F_i, M_i, P_i, and RF_i, as well as data on average weights of fish at each age, total yields from the ocean and river fisheries for a given number of recruits (R) can be calculated. Henry (1971) gives estimates of F_i and P_i for various values of M_i as well as values for RF_i for 1961 brood Spring Creek and Kalama fish and 1962 brood Kalama fish. Lack of river recoveries of 5-year-old fish prevented estimates of these values for 1962 brood Spring Creek chinook salmon. Henry also lists average weight data, by age, for both

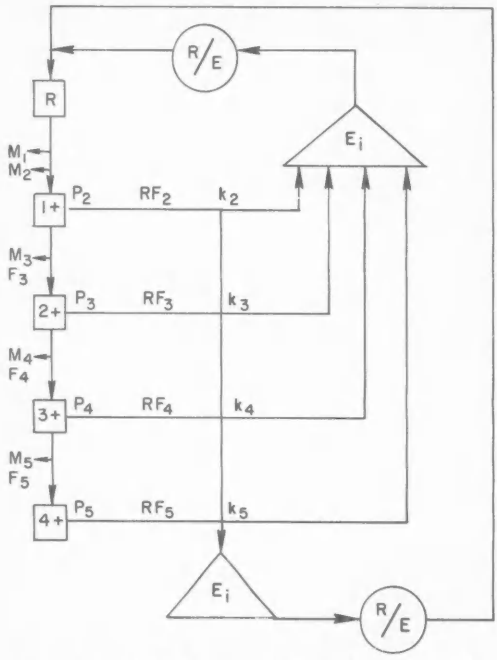

FIGURE 11.—Block diagram of a population model for Columbia River fall chinook salmon (adapted from Shapiro and Andreev, 1969).

M_i = natural mortality rate.
F_i = ocean fishing mortality rate.
RF_i = river fishing mortality rate.
P_i = probability of being a spawner.
k_i = percentage of spawners taken for artificial reproduction.
E_i = effective fecundity/1,000 eggs.
R = number of recruits.
1+, 2+, 3+, 4+ = age of fish.

the ocean and river recoveries of these two stocks of fish.

The procedures followed in these analyses were: given a certain number of recruits (1,000) and a certain M_i (natural mortality) value, and assuming $M_2 = M_3 = M_4$, I calculated the total yield for all ages (numbers caught × average weight) from both the ocean and river fisheries using the P_i values (where P_i is the proportion of the ocean population entering the river to spawn) for the M_i as given by Henry (1971). I let the P_i and RF_i values (where RF_i is the river fishing mortality) remain constant but varied the F_i's (where F_i is the ocean fishing mortality) from 0 to 1.8. This procedure resulted in a 3-dimensional yield diagram (i.e., F_3, F_4, and F_5). The computations were done on an IBM 1130[1] computer and I wrote the program so the computed yields were plotted directly in even yield planes by a CalComp plotter.

Regardless of the natural mortality rate assumed for these computations, it appears that total yields under actual conditions were below the potential yields for both Spring Creek and Kalama fall chinook. In Figure 12 are depicted the calculated maximum potential yields for various values of natural mortality (M_i) and the ocean fishing values (F_i) needed to achieve these maximum yields as well as the calculated yields based on estimated fishing mortality rates for various values of M as given by Henry (1971). It is only with the higher levels of natural mortality (>0.60) or with the 1962 brood Spring Creek fish that a troll fishery on the 3-year-olds (F_3) would have increased yield. At all levels of natural mortality shown, maximum yield required maximum troll fishing effort on the 5-year-old fish (F_5).

The calculated total yield varied considerably depending on the F and M values used. The 3-dimensional outputs for $M = 0.24$ and $F_i = 0$ to 1.8 for the two hatcheries for the 1961 brood year are shown in Figures 13 and 14. I have included a yield diagram for each stock to show the differences in yield that can be generated in this type of analysis as well as to emphasize the differences between these two groups of salmon. The calculated yield planes shown in these figures are actually planes of equal yield passing through the block diagrams. Each yield plane shown consists of points that represent all possible combinations of ocean fishing mortality (F_3, F_4, and F_5)—such that total yield will equal the value shown. In Figure 13, for 1961 brood Spring Creek fish ($M = 0.24$), the maximum yield is at point A ($F_3 = 0$, $F_4 = 0$, and $F_5 = 1.8$) and is slightly over 6,300, the same value as shown in Figure 12. Yield diagrams calculated for $M = 0.96$ were similar to

[1] Use of trade names does not imply endorsement by the National Marine Fisheries Service.

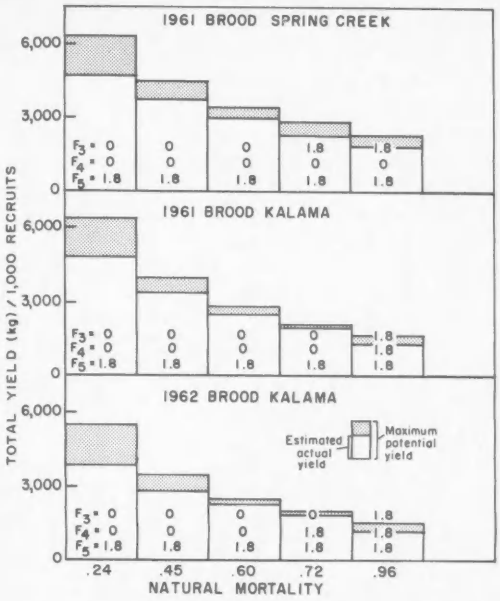

FIGURE 12.—Calculated maximum potential yields (kilograms) per 1,000 recruits for the 1961 brood Spring Creek and Kalama and the 1962 brood Kalama hatchery fall chinook salmon compared with yields calculated for estimated rates of actual ocean fishing mortality (F values shown are those producing maximum potential yields).

those shown except that they depicted lower yields, as would be expected with a higher natural mortality. Similar analyses also were made from the 1962 brood data, but those yield diagrams are not depicted.

In a similar manner to that shown for obtaining the maximum yield, the calculated total yield for any combination of F_3, F_4, and F_5 could be estimated from these graphs. However, the purpose of these graphs is not to estimate single yield values but rather to show the overall effect on yield of varying values of F_3, F_4, and F_5. Thus, Figure 13 shows that the total yields diminish as F_3 and F_4 increase but that F_5 has little effect on total yield. Under these conditions, any troll fishing on 3- and 4-year-old fish would reduce the total yield.

It might be well to re-emphasize that these calculations are based on the assumption of a constant M for the period analyzed. Variations in M during this period would, of course, affect the calculated total yield depending on when the variations occurred and their magnitude. However, a differential M before entry into the troll fishery, i.e., at age 2 and younger, would not affect this analysis.

There is considerable variation in the two yield diagrams, and the reader will have to examine each figure to see in detail the effect of varying levels of troll fishing for that particular brood and level of natural mortality. In general, at the lower levels of natural mortality ($M = 0.24$), increased troll fishing on the younger age group ($2+$ and $3+$) results in reduced yields, whereas the reverse of this generally occurs at the higher level of natural mortality ($M = 0.96$). In other words, at the younger ages and the lower natural mortalities it appears that the rate of growth exceeds the loss due to natural mortality and, consequently, yield is increased by letting the salmon reach an older age before harvesting them. It should be pointed out that even if no fish had been caught in the ocean, the number returning to the river would have been less than the sum of river entry and ocean catch since some of the fish caught in the ocean fishery would have died from natural causes.

The values of M and F that I used, although arbitrary, are believed to cover the range of realistic possible values. Obviously, any values of M could be inserted into the program, but it was felt that $M = 0.24$ and $M = 0.96$ would depict extremes. Also, F_i values greater than 1.8 could be used, but I arbitrarily limited them at this upper boundary because F values of 1.8 considerably exceed any of the F values calculated for either the 1961 or 1962 brood data (Henry, 1971).

The calculated total yields for 1961 and 1962 brood Spring Creek and Kalama fall chinook salmon for various values of natural mortality —if troll fishing could be restricted to only one age group; i.e., troll fishing on only the 3-, 4-, or 5-year-old fish—are shown in Figures 15 and 16. The values for river fishing intensity and proportion spawning are the same as used in the previous analyses. The yields shown are the

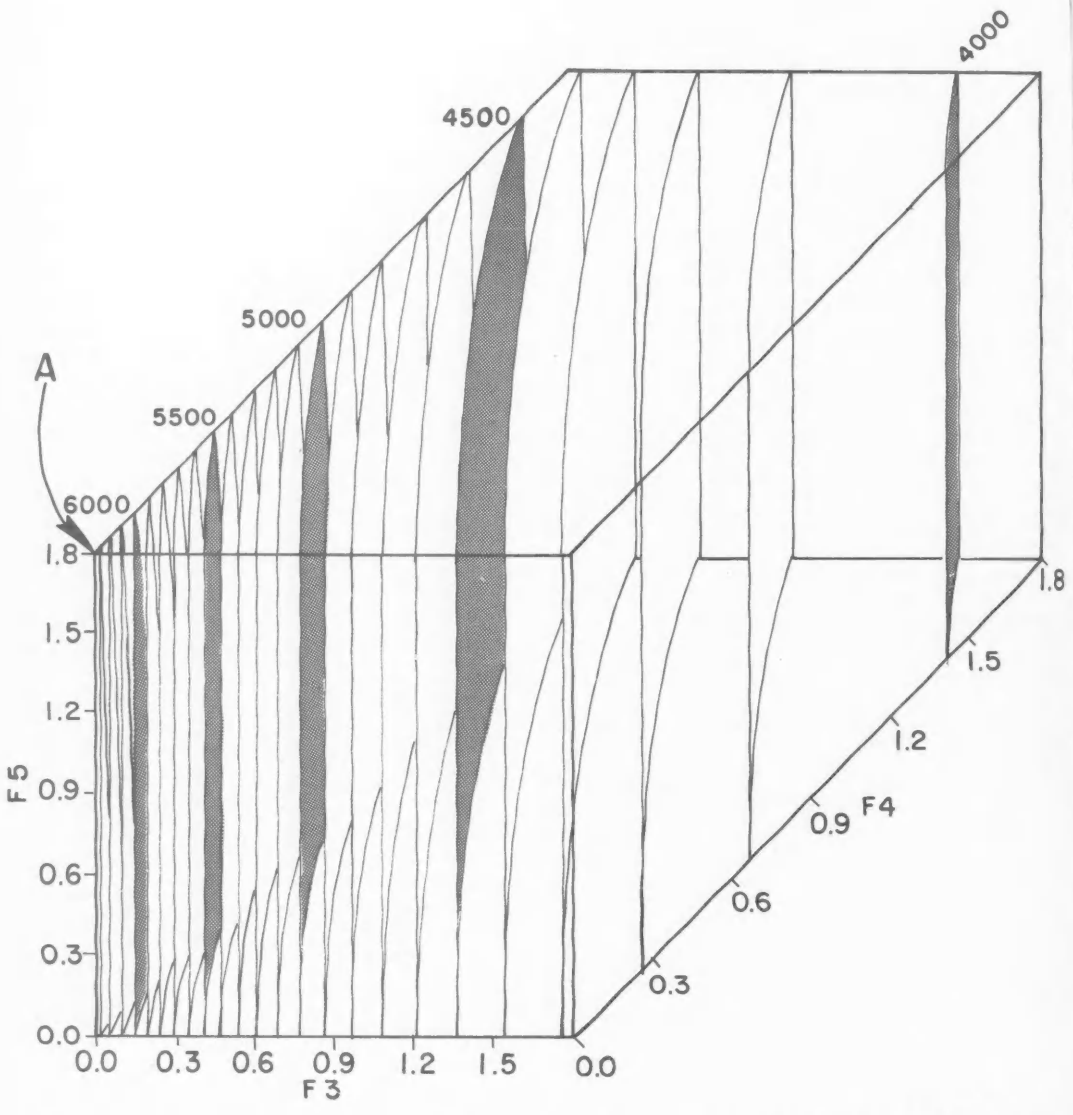

FIGURE 13.—Calculated total yield diagrams (in kilograms per 1,000 recruits) for the 1961 brood Spring Creek hatchery fall chinook salmon with constant natural mortality ($M = 0.24$), varying ocean troll fishing mortality rates (F_3, F_4, and F_5), and the proportion spawning and river fishing intensity remaining constant. Yields are shown by 100-kilogram plane intervals.

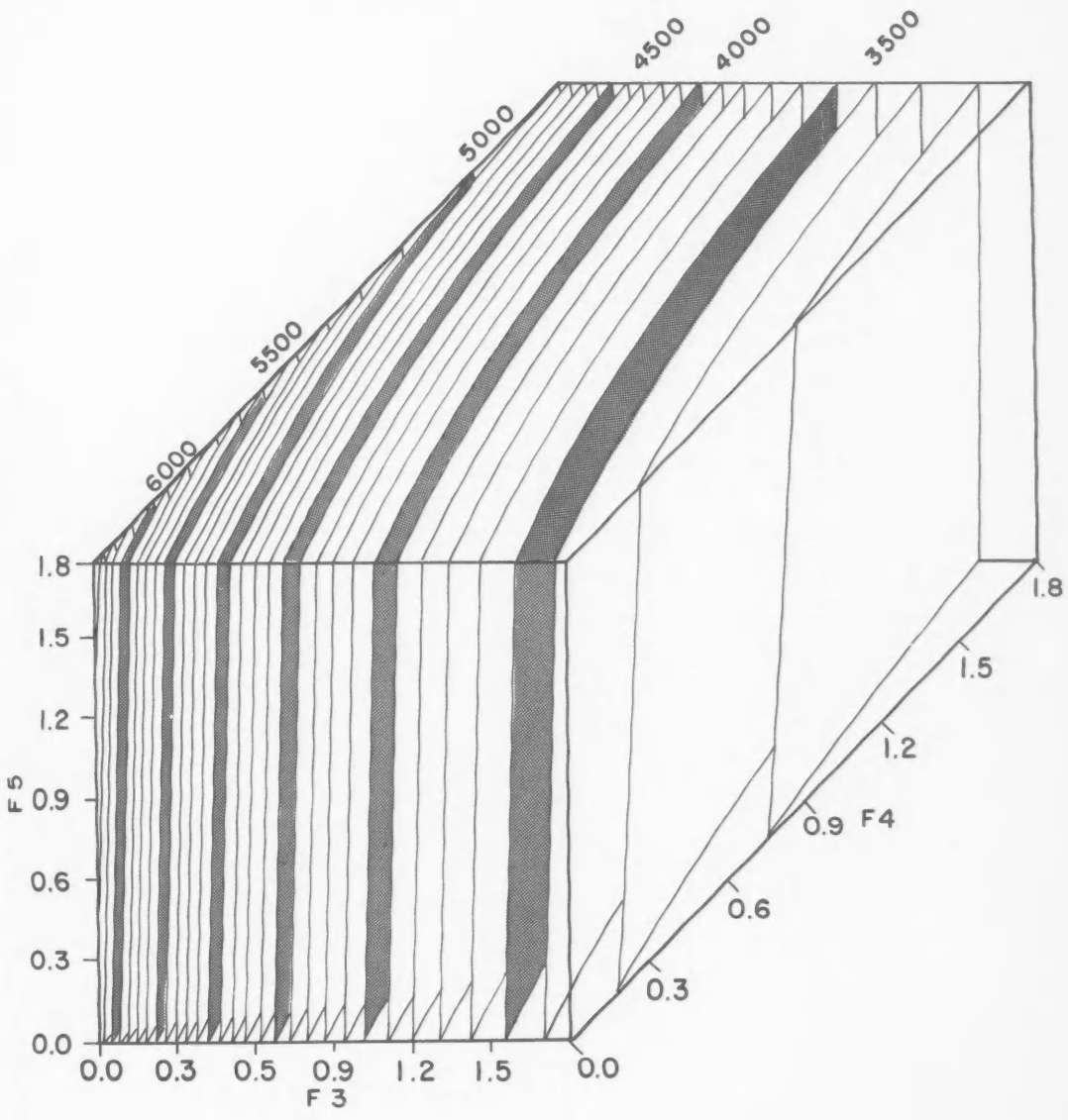

FIGURE 14.—Calculated total yield diagrams (in kilograms per 1,000 recruits) for the 1961 brood Kalama hatchery fall chinook salmon with constant natural mortality ($M = 0.24$), varying ocean troll fishing mortality rates (F_3, F_4, and F_5), and the proportion spawning and river fishing intensity remaining constant. Yields are shown by 100-kilogram plane intervals.

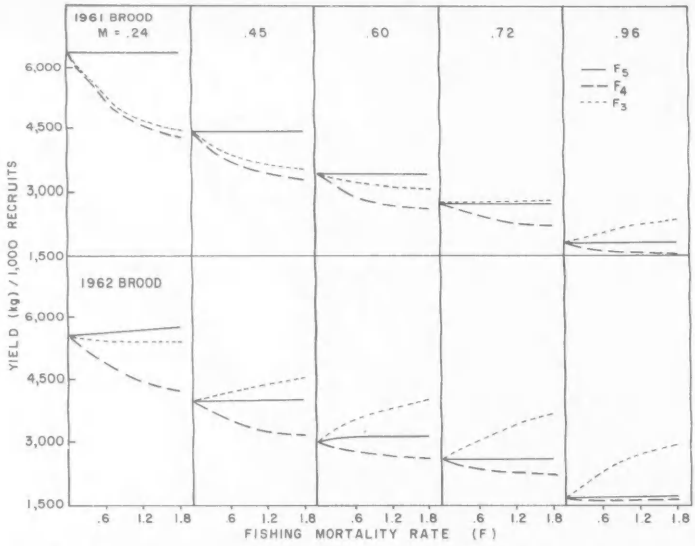

FIGURE 15.—Calculated total yields (in kilograms) for 1961 and 1962 brood Spring Creek hatchery fall chinook salmon for different natural mortality rates and fishing on only one age group at a time.

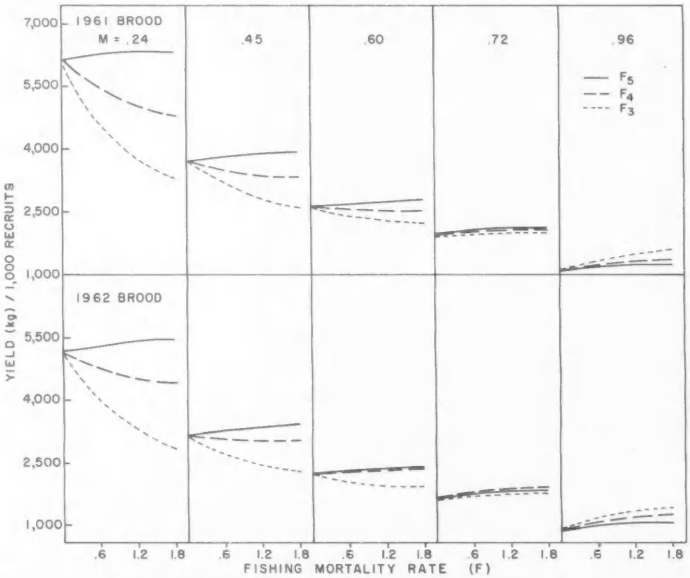

FIGURE 16.—Calculated total yields (in kilograms) for 1961 and 1962 brood Kalama hatchery fall chinook salmon for different natural mortality rates and fishing on only one age group at a time.

same as would be observed by reading along the F_3, F_4, and F_5 axes in Figures 13 and 14. It is apparent from these data that at any level of natural mortality (M_i), as fishing mortality is increased on the 5-year-old fish (F_5) (with F_3 and $F_4 = 0$), total yield increases, although slightly. For the Spring Creek data (Figure 15), any increase in F_4, with the other two F values $= 0$, would result in reduced yield. For Kalama fish (Figure 16), for both broods at $M = 0.72$ and higher, total yield would increase with an increase in any of the F values. In general, troll fishing on the age 3 and age 4 Spring Creek and Kalama fall chinook salmon tends to reduce total yield for M_i values less than 0.82, except for the 1962 brood Spring Creek fish. For these fish it appears that growth was insufficient to compensate for natural mortality losses of 4-year-old fish, even at a natural mortality rate of $M = 0.45$. Thus, yield was increased by harvesting them as 3-year-olds in the troll fishery (F_3).

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SELECTION OF SPAWNING SITES BY SOCKEYE SALMON IN SMALL STREAMS

DAVID T. HOOPES[1]

ABSTRACT

This study was undertaken in three small western Alaska streams to identify factors that influence selection of spawning sites by sockeye salmon. Temporal and spatial distribution patterns were relatively constant from year to year despite large fluctuations in the number of spawners. The selection of a spawning site was more closely related to composition of the stream bottom than to gradient, water depth and velocity, or cover.

The selection of spawning sites by salmon and the factors that influence selection bear directly on the problem of estimating the carrying capacities of spawning grounds. Such estimates cannot be developed for returning adults without knowledge of what constitutes an acceptable spawning area. In this study I relate the distribution of spawning sockeye salmon, *Oncorhynchus nerka*, in three small streams to the physical characteristics of the streams. The work reported was done at Brooks Lake, Alaska, in 1959, 1960, and 1961 and is one phase of an overall investigation by the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) on the freshwater ecology of sockeye salmon.

The three study streams, Hidden, Up-a-tree, and One Shot Creeks, are lateral[2] tributaries of Brooks Lake (Figure 1). Hidden Creek enters Brooks Lake in the southeastern shore about 10 km from the outlet, Brooks River. The other two streams lie between Brooks River and Hidden Creek. Up-a-tree Creek, the longest lateral stream in the Brooks Lake system, enters the lake at the southeastern corner; One Shot Creek, the shortest of the major spawning tributaries, flows into the lake on the south shore not far from Hidden Creek. Some physical features of the portions of the three streams accessible to salmon are presented in Table 1. Included in the table is the pool-riffle ratio, an indicator of the proportion of stream length composed of pools. What constitutes a pool is somewhat subjective, but I considered a pool to be a place where the stream was deeper and wider than average, the current was appreciably slower than immediately upstream or downstream, and hiding places for fish were more extensive than in adjacent parts of the stream.

The three streams were alike in two significant aspects—volume of flow and presence of beaver dams. Flows in each stream varied from 0.23 to 0.34 m^3s (cubic meter per second) (8.2 to 12.1 cfs) throughout the spawning season except for some short periods of higher flows during freshets. Beaver dams blocked the upstream migration of salmon except during brief periods of unusually high water.

DISTRIBUTION OF SPAWNERS

The distribution of adult sockeye salmon was observed closely and recorded from the time fish arrived off the stream mouths until they had all spawned. I recorded the number of fish ascending the streams each day and the distribution of spawners along each stream on an average of every 3 days.

Sockeye salmon school off the mouths of tributaries to Brooks Lake 1 to 3 weeks before ascending the streams to spawn (Hartman and

[1] National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, AK 99821.

[2] The term "lateral tributaries" refers to streams entering a lake from shores that lie roughly parallel to the lake's long axis.

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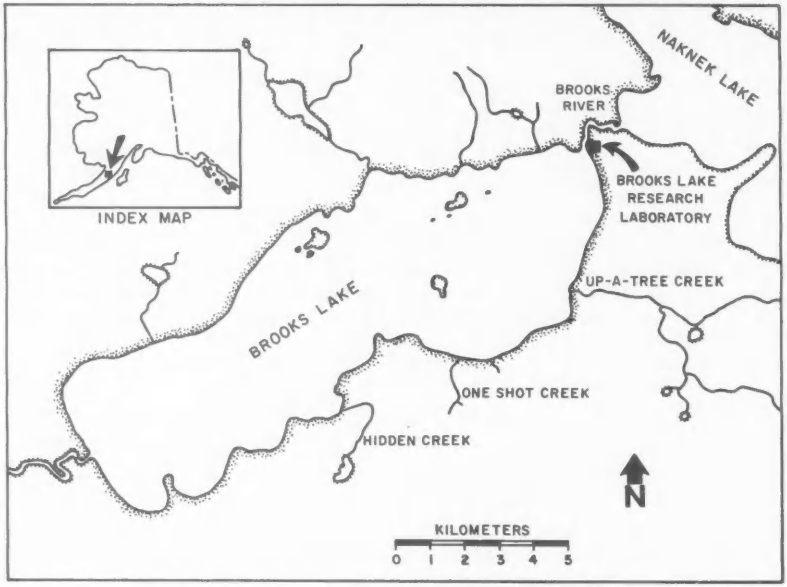

FIGURE 1.—Brooks Lake, Alaska, showing three lateral tributaries where spawning sockeye salmon were studied in 1959, 1960, and 1961.

Raleigh, 1964). I observed fish joining schools off the stream mouths even after some fish had entered the streams and begun spawning. These late-arriving fish usually spent several days in the school before they ascended the stream.

In some years all adult sockeye salmon that entered the study streams were passed through weirs. Weirs were operated at Up-a-tree and One Shot Creeks in 1961 (Table 2) and at Hidden Creek in 1959, 1960, and 1961 (Table 3). To insure that all fish in the run were counted, the weirs were closed when fish first appeared off the stream mouths. The fish were allowed to pass upstream through a counting gate whenever 10 or so appeared immediately downstream from the weir.

Although spawning sockeye salmon were constantly present in each study stream for several weeks, they tended to enter the streams in waves or pulses. Fish entered Hidden Creek in several distinct waves in 1959 and 1960 but not in 1961 (Table 3). However, the weir records for Up-a-tree and One Shot Creeks suggest the presence of more than one major influx of spawners in

TABLE 1.—Watershed area, total length, and physical characteristics of portions of streams accessible to salmon in Hidden, Up-a-tree, and One Shot Creeks, tributaries to Brooks Lake, Alaska.

Stream	Watershed area (km^2)	Total length (km)	Portion accessible to salmon					
			Stream length (km)	Range of stream width (m)	Pool-riffle ratio	Range of pool depths (cm)	Range of riffle depths (cm)	Percent gradient in spawning areas (*range*)
Hidden Creek	28	13	3.9	3-6.0	4:6	50- 80	15-30	0.74-1.45
Up-a-tree Creek	75	24	8.0	3-4.5	3:7	60-100	25-35	0.36-0.72
One Shot Creek	13	6.5	3.8	3-4.0	3:7	60- 90	25-35	0.84-1.30

TABLE 2.—Number of sockeye salmon passed upstream through the weirs each day and cumulative upstream count at Up-a-tree and One Shot Creeks, 1961.

Stream and date	No. of fish through weir	Cumulative count	Stream and date	No. of fish through weir	Cumulative count
Up-a-tree Creek			One Shot Creek		
July 28	1	1	July 30	1	1
29	0	1	31	10	11
30	135	136			
		[1]521	Aug. 1	14	25
31	[2]121	642	2	146	171
			3	6	177
Aug. 1	1	643	4	9	186
2	35	678	5	3	189
3	0	678	6	0	189
4	0	678	7	0	189
5	10	688	8	85	274
6	3	691	9	1	275
7	0	691	10	0	275
8	26	717	11	4	279
9	59	776	12	11	290
10	0	776	13	0	290
11	9	785	14	0	290
12	2	787	15	1	291
13	3	790	16	0	291
14	19	809	17	0	291
15	10	819	18	5	296
16	0	819	19	0	296
17	12	831	20	4	300
18	0	831	21	0	300
19	0	831	22	0	300
20	0	831	23	0	300
21	0	831	24	0	300
22	0	831	25	0	300
23	0	831	26	0	300
24	0	831	27	1	301
25	0	831	28	2	303
26	0	831	29	0	303
27	1	832	30	2	305

[1] At 7:30 a.m. on July 30 the Up-a-tree Creek weir was washed out because of high water. The weir was replaced and a stream survey made on July 31 after the water receded and cleared. An estimate of 521 fish was obtained. This figure was used for subsequent cumulative counts.
[2] Counted upstream after survey.

these two streams in 1961 (Table 2). Three distinct waves of spawners were observed in studies on nearby Brooks River by Hartman, Merrell, and Painter (1964).

The distribution of spawners over the length of each stream was determined from repeated counts of occupied redds in survey sections which were established for measuring stream gradients.[3] The counts were summed by section and totaled for the entire stream. The percentage of this total occurring in each section was calculated for the year, and these percentages were used as indicators of the distribution of each year's run. Distribution was not uniform among the three study streams during the 3 years of this study but was generally consistent for each stream (Figures 2, 3, 4) despite marked differences between years in the number of spawners (Table 4).

In 1959, when occupied redd sites were counted at 2-day intervals, the distribution of spawners in Hidden Creek changed very little after the first week. Counts were combined to show the similarity in distribution of occupied redds at the end of the first, second, and third week of spawning (Figure 5). By the end of the first week (early period), 2,625 sockeye salmon had ascended the stream to select redd sites and spawn. An additional 1,239 fish entered and began to spawn during the second week (middle period), and 694 more entered during the third week (late period). Thus, substantial numbers

[3] These survey sections will be described in more detail later. They consist of 100- to 200-m-long segments of stream channel extending from the mouths of the study streams to the first beaver dam judged to be normally impassable to migrating salmon.

TABLE 3.—Number of sockeye salmon passed upstream through the weir each day and cumulative upstream count at Hidden Creek, 1959, 1960, and 1961.

Date	1959		1960		1961	
	No. of fish through weir	Cumulative count	No. of fish through weir	Cumulative count	No. of fish through weir	Cumulative count
August						
9	--	--	--	--	38	38
10	1,240	1,240	--	--	0	38
11	0	1,240	--	--	39	77
12	0	1,240	--	--	1	78
13	547	1,787	--	--	383	461
14	40	1,827	23	23	417	878
15	574	2,401	1,216	1,239	0	878
16	224	2,625	269	1,508	0	878
17	0	2,625	6	1,514	8	886
18	1,217	3,842	42	1,556	130	1,016
19	0	3,842	0	1,556	0	1,016
20	0	3,842	0	1,556	0	1,016
21	0	3,842	319	1,875	0	1,016
22	22	3,864	158	2,033	0	1,016
23	0	3,864	0	2,033	0	1,016
24	0	3,864	110	2,143	0	1,016
25	0	3,864	43	2,186	7	1,023
26	0	3,864	1	2,187	46	1,069
27	0	3,864	15	2,202	3	1,072
28	694	4,558	37	2,239	0	1,072
29	--	--	10	2,249	1	1,073
30	--	--	26	2,275	0	1,073
31	--	--	--	--	1	1,074
September						
1	--	--	--	--	4	1,078
2	--	--	--	--	0	1,078
3	--	--	--	--	0	1,078
4	--	--	--	--	0	1,078
5	--	--	--	--	13	1,091

TABLE 4.—Sockeye salmon escapements into Hidden, Up-a-tree, and One Shot Creeks in 1959, 1960, and 1961.

Stream and year	Method of enumeration	No. of fish in escapement[1]
Hidden Creek		
1959	Weir count	4,558
1960	Weir count	2,275
1961	Weir count	1,078
Up-a-tree Creek		
1959	Stream survey[2]	542
1960	Stream survey	1,334
1961	Stream survey and weir	653 (832)
One Shot Creek		
1959	Stream survey	246
1960	Stream survey	269
1961	Stream survey and weir	221 (305)

[1] Figures in parentheses are weir counts.
[2] Highest single count during any one season.

of fish ascended the stream and occupied redd sites while other fish were already spawning. Some late fish spawned adjacent to previous arrivals, and others continued on to the upstream spawning areas. This distribution of spawners was not measurably altered by differences in their numbers, as evidenced by the distribution throughout the season of the considerably fewer fish in 1961.

Although the distribution of spawners from year to year varied more in Up-a-tree than in Hidden Creek, Up-a-tree Creek had areas of consistently high and consistently low spawning density (Figure 3). More spawners entered Up-a-tree Creek in 1960 than in 1959 or 1961, and the 1960 spawners were distributed more uniformly along a greater length of stream than either the 1959 or 1961 spawners. In 1961, relatively few fish spawned in the lower sections of the stream.

The distribution and number of spawners in One Shot Creek was similar for the 3 years of the study (Figure 4, Table 4)—here spawners consistently concentrated in the upper and lower ends of the stream.

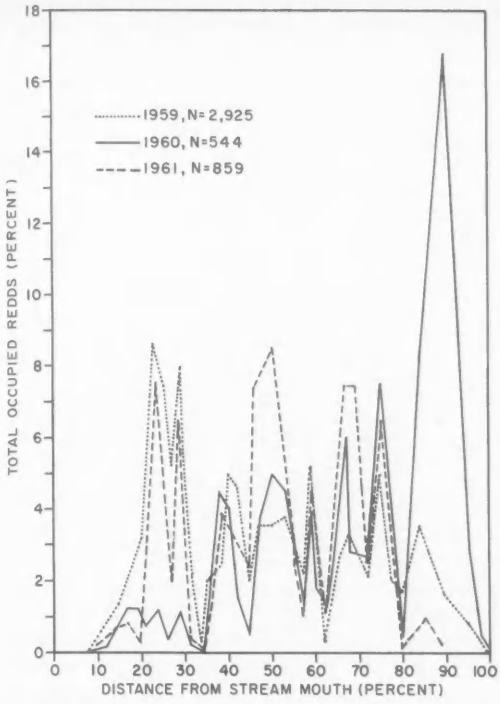

FIGURE 2.—Distribution of redds occupied by sockeye salmon in Hidden Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

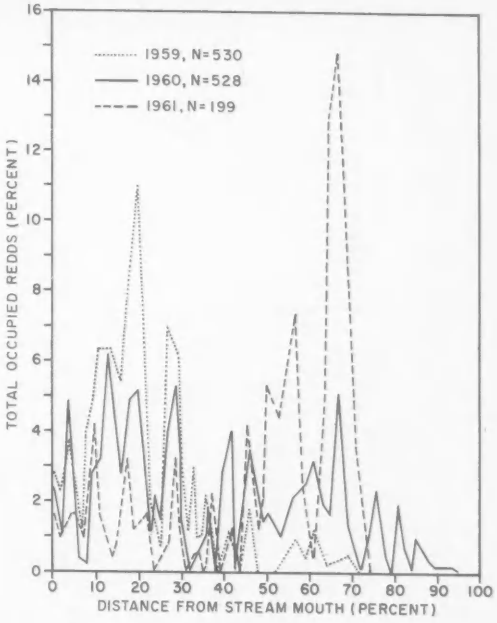

FIGURE 3.—Distribution of redds occupied by sockeye salmon in Up-a-tree Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

PHYSICAL CHARACTERISTICS OF STUDY STREAMS IN RELATION TO SPAWNING

To determine relationships between the location of spawning sites and physical characteristics of the streams, I measured the gradient, size composition of the bottom materials, and water depth and velocity of spawning areas in the three streams. Velocity and volume of streamflow, stream width, and stream gradient are known to affect the size composition of materials in the streambed, but velocity is considered to be the dominant factor (Krumbein and Pettijohn, 1938; Rubey, 1938; Hjulstrom, 1939; Krumbein and Sloss, 1951). A reduction in stream gradient is accompanied by a reduction in water velocity and in the average size of bottom particles.

STREAM GRADIENT

Gradients were measured in each study stream from the mouth to the first beaver dam judged normally impassable to migrating salmon. Gradients were calculated between convenient points (stations) that were 100 to 200 m apart along the stream. The relative elevation of the water surface was measured with a surveyor's level, and the distance between stations was measured along the center of the streambed with a surveyor's chain. Stream width was also measured at each station. The survey sections were numbered consecutively upstream from the mouth of each creek.

Survey sections were often too long to reveal variations in gradient and distribution of spawn-

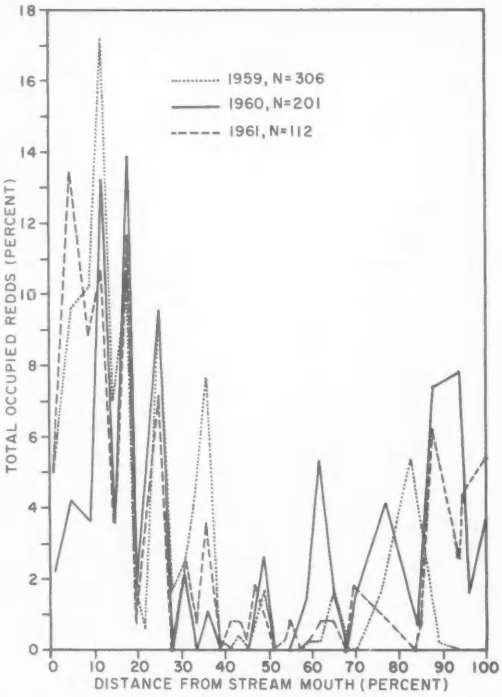

FIGURE 4.—Distribution of redds occupied by sockeye salmon in One Shot Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

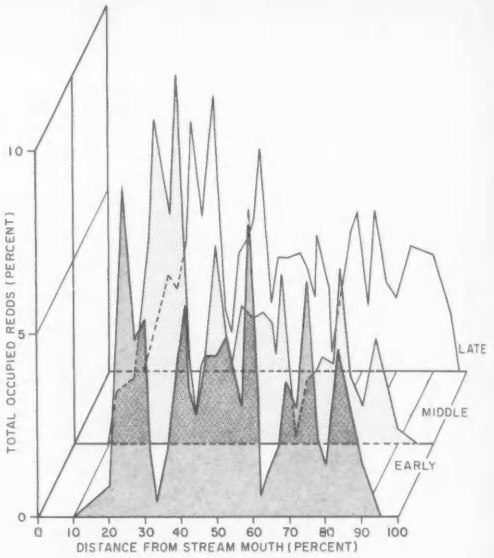

FIGURE 5.—Temporal and spatial distribution of redds occupied by sockeye salmon during the early, middle, and late periods of the 1959 spawning season in Hidden Creek, Brooks Lake, Alaska.

ers in great detail. For example, some had so many steep runs and falls that the average gradient appeared to be too high for spawning, although the sections contained one or two short reaches of stream with gradients acceptable to spawning fish. Other sections had long reaches of generally too low gradient but had one or two short steep falls, so that little acceptable spawning ground was actually available even though the average gradient appeared suitable for spawning. Despite these problems in methodology, after comparing the density of spawning females and stream gradients section by section in the three study streams for all 3 years, I found that little or no spawning occurred in areas having average gradients of less than 0.5% or more than 2.0%.

SIZE OF STREAMBED MATERIALS IN SELECTED SECTIONS

I made detailed studies of bottom composition in eight of the sections surveyed for gradient.[4] Sections were selected for these detailed studies on the basis of their relative amounts of use by spawning salmon so that areas having high and low spawning densities could be compared. Two sections with high and two with low densities of spawners were selected in Hidden Creek, and one each was selected in Up-a-tree and One Shot Creeks.

From six to nine samples of the streambed were collected in each of the eight sections. The samples were taken from both pools and riffles at locations where salmon spawned in 1959. Each sample consisted of the top 20 to 30 cm of bottom materials (gravel and sand) from an area 1 m^2. The material was removed from the

[4] Observations were also made on water depth and velocity and availability of streambank cover.

streambed with a shovel and placed in a cotton soil sample bag. It was later washed into individual 19-liter tins, drained, and allowed to air dry. The dried samples were separated into 10 size classes by passing them through a stacked series of square-meshed 20-cm U.S. Standard sieves. After the sample was placed on the top sieve, the series was agitated for 10 min in a hand-powered portable sieve shaker. The materials retained on each sieve were weighed to the nearest gram on a triple-beam trip scale.

I describe the particle size distribution of the streambed by relating the percent of the total sample weight retained on each sieve to the logarithm of its mesh size. This method of analysis is described more fully by Spangler (1951) and by the American Society for Testing Materials (1958).

Because the particle composition of streambed samples from pools and riffles was so similar within each section, I combined the data by section. I then derived a cumulative size distribution for each section by summing the weights retained by each sieve size in all samples for a section. These data were used to construct cumulative distribution curves with which I could compare the composition of the stream bottom in sections of high spawning density (Figure 6) with that in sections of low spawning density (Figure 7).

The curves for sections of high spawning density (Figure 6) show that bottom composition was quite similar in all three streams. The only difference among the four sections was the slightly higher percentage of small particles and the somewhat lower percentage of large particles in section 9 of Hidden Creek, as evidenced by the lateral displacement toward the left of the composition curve for this section.

The cumulative curves for sections with low spawning density (Figure 7) showed that particle size distribution was similar in three of the sections (one from each stream) but quite different in the fourth section (Hidden Creek, 2). It is clear that spawner density was low in Hidden Creek in areas where particle sizes were either very large or very small.

Sockeye salmon spawned most frequently in areas where the particles were intermediate in size. In sections of high spawning density and intermediate gradient, cobbles larger than 7.6 cm in diameter made up about 6% of the bottom, cobbles from 2.5 to 7.6 cm about 50%, particles 1.3 to 2.5 cm about 20%, and particles less than 1.3 cm the remainder (Figure 8A). The bottom in sections of low spawning density and high gradient was made up of almost 40% cobbles exceeding 7.6 cm in diameter and contained very little material less than 2.5 cm in diameter (Figure 8B). The bottom in sections of low spawn-

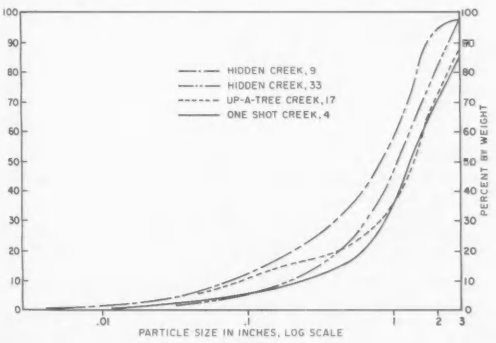

FIGURE 6.—Curves of cumulative particle size distribution in four sections with high-spawning density, Hidden Creek sections 9 and 33, Up-a-tree Creek section 17, and One Shot Creek section 4. All four sections had intermediate stream gradients.

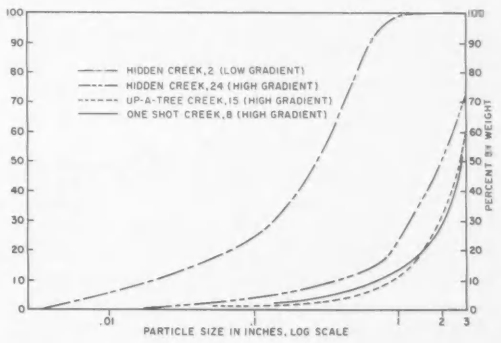
HIDDEN CREEK, 2 (LOW GRADIENT)
HIDDEN CREEK, 24 (HIGH GRADIENT)
UP-A-TREE CREEK, 15 (HIGH GRADIENT)
ONE SHOT CREEK, 8 (HIGH GRADIENT)
PERCENT BY WEIGHT
PARTICLE SIZE IN INCHES, LOG SCALE

FIGURE 7.—Curves of cumulative particle size distribution in four sections with low-spawning density, Hidden Creek sections 2 and 24, Up-a-tree Creek section 15, and One Shot Creek section 8. All of the sections had high gradients except Hidden Creek section 2, which had low.

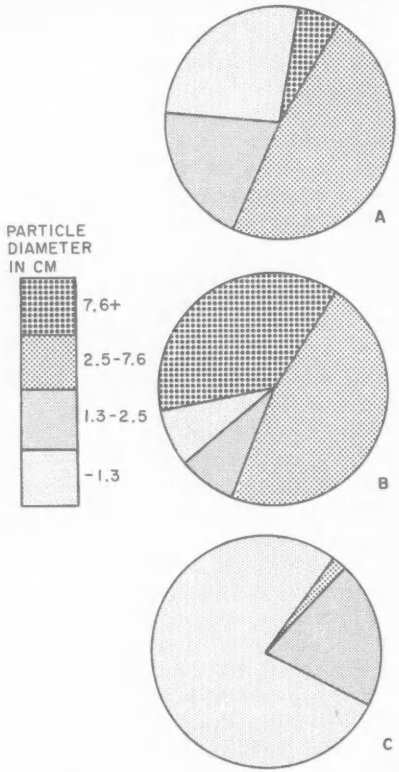

FIGURE 8.—Particle composition by percent weight of bottom materials in study sections having (A) high spawning density and intermediate gradient, (B) low spawning density and high gradient, and (C) low spawning density and low gradient.

ing density and low gradient contained 80% particles under 1.3 cm in diameter (Figure 8C).

WATER DEPTH AND VELOCITY

Water depth and velocity were measured in 1960 in each of the eight study sections (Table 5). Three to five transects about equidistant from each other were laid out across the stream in each section. Velocity and depth were measured at about 0.3-m intervals along these transects with a Gurley impeller-type current meter[5] mounted on a graduated rod and set at 12 cm above the streambed, described as "fish depth" for Pacific salmon.[6] Volume of flow was computed from the velocity and depth data collected. The values presented are assumed to reflect conditions normally encountered by fish selecting spawning sites in the study sections, although pronounced changes in water depth and velocity may occur briefly during the spawning season as a result of heavy rains. Sections with high and low densities of spawners often had similar water depths and velocities (Table 5: Depths—Hidden Creek, section 9 versus 24; One Shot Creek, section 4 versus 8. Velocities—Hidden Creek sections 9 and 33 versus Up-a-tree Creek section 15 and One Shot Creek section 8).

[5] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

[6] J. S. Chambers, R. T. Pressey, J. R. Donaldson, and W. R. McKinley. Washington State Department of Fisheries, Annual Report, 1954, submitted to U.S. Army Corps of Engineers, 145 p.

TABLE 5.—Average depth, velocity, and volume of flow in sections of high and low spawning densities of Hidden, Up-a-tree, and One Shot Creeks, Brooks Lake, Alaska, 1960.

Stream and section	Level of spawning density	Average depth (cm)	Water velocity (mps)	Water velocity (fps)	Volume of flow (m^3s)	Volume of flow (cfs)
Hidden Creek						
9	High	15	0.59	1.9	0.27	9.6
33	High	23	0.45	1.5	0.31	11.1
24	Low	15	0.70	2.3	0.25	8.9
2	Low	28	0.39	1.3	0.28	10.0
Up-a-tree Creek						
17	High	24	0.36	1.2	0.29	10.3
15	Low	23	0.47	1.5	0.31	11.1
One Shot Creek						
4	High	32	0.35	1.1	0.37	13.2
8	Low	28	0.54	1.8	0.44	15.7

FACTORS AFFECTING SPAWNING SITE SELECTION

Salmon and trout usually spawn in a specific type of microenvironment within a broadly uniform environment. One such type of microenvironment occurs at the downstream ends or tails of pools, just upstream from the point where the flow breaks over the lip of the pool into the riffle below (Needham and Taft, 1934; Schultz and students, 1935; Smith, 1941; White, 1942; Briggs, 1953; Shapovalov and Taft, 1954). Riffles may also contain microenvironments attractive to spawning salmon[7] (Belding, 1934; Burner, 1951; Needham and Vaughan, 1952; Briggs, 1953; see also footnote 6.)

Variations in streambed slope are important in the selection of spawning sites because these variations cause exchange in intragravel and stream water (Vaux, 1962) and affect the stability of the bottom. In pools, spawning sites were usually located where the bottom sloped upward slightly in the direction of flow, as in pool tails. Even in riffles, fish observed during this study seldom constructed redds where the bottom sloped steeply but rather chose gently sloping sites where the excavated tailspill provided a slight rise. The preferred streambed was also nearly level across the stream, although moderate to steep lateral inclines were occasionally used in crowded areas.

In 1959, sockeye salmon first entered and began spawning in Hidden Creek on August 11. On August 13, I marked 14 redds in an area of high spawning density after taking detailed notes on the exact location of each spawning site and the features of the immediate environment. I assumed that the first fish in an area selected the preferred sites, so that these 14 sites represented preferred habitat. All of the sites were at or near the tails of pools and along the bank adjacent to the main streamflow. I observed the sites until August 25, when high water precluded further study.

[7] J. S. Chambers, G. H. Allen, and R. T. Pressey. Washington State Department of Fisheries, Annual Report, 1955, submitted to U.S. Army Corps of Engineers, 175 p.

Observations in the immediate vicinity of the 14 study redds showed that late-arriving fish spawned upstream from the initial redd at the tail of each pool. When the pool was filled with redds for its entire length and pool width permitted two or more redds side by side, late arrivals chose spawning sites sequentially upstream, again beginning at the tail but across the stream from the original site. No salmon spawned in unstable gravels usually associated with the shallow sides of pools.

Riffles made up 60 to 70% of the stream length accessible to salmon in the three study streams, and many fish spawned in these riffles. As in the pools, spawning salmon preferred definite parts of the riffles. The first fish invariably chose sites along the deeper side and higher bank. Salmon also preferred certain riffles over others. Short riffles with water of moderate depth and flow were used as readily as pool tails. Long shallow riffles with some cover along adjacent banks were occupied next. The last sites used were those in long shallow riffles without nearby pools or cover.

The significance of cover in the selection of a spawning site by sockeye salmon is hard to evaluate. Hourston and MacKinnon (1957) found that pink salmon, *O. gorbuscha*, spawning in an artificial channel selected sites adjacent to cover rather than those distant from cover. I frequently observed that sockeye salmon, especially those that arrived early when a wide choice of sites was available, selected a site that had good cover. The absence of cover did not necessarily prevent early spawners from selecting a particular site, but given two adjacent locations apparently equal with regard to water depth and flow and gravel composition, the fish tended to select the site nearer to cover. Favored sites were near deeply undercut banks, banks overhung with tall grass and herbaceous plants, holes washed under tree roots, log and brush jams, and deep pools.

Cover that attracts alarmed fish may not actually afford protection, because concealment alone does not insure safety. I have observed brown bears, *Ursus gyas*, systematically search for salmon under overhanging vegetation and undercut banks. In my three study streams,

cover that would protect a salmon from bears was quite scant, and even when such cover was available, alarmed fish often sought the shaded area provided by overhanging herbs and grasses as refuge rather than places of comparatively greater security such as undercut banks and logs.

The selection of a site by a spawning sockeye salmon seemed to be more closely related to the composition of the stream bottom than to any other single factor studied. Work done with fish closely related to salmon supports this view (Hobbs, 1940; Fabricius, 1950; Fabricius and Gustafson, 1954; Needham, 1961). This preference by salmon for areas having bottom materials of intermediate composition explains why the density of spawners was high in sections with moderate gradient and low in sections with either high or low gradient. When more desirable bottom material was lacking, fish spawned in excessively coarse material (higher gradients) before excessively fine (lower gradients). In this respect, my observations indicated that gradient was related to the selection of spawning sites by sockeye salmon. The observations by Trautman (1942) and Huet (1949, 1959) showing that distribution of several species of fish permanently resident in lotic environments is closely related to stream gradient may well have resulted from a preference by those fish for a particular substrate.

Factors other than physical conditions in the spawning grounds may also influence the selection of redd sites by sockeye salmon. Briggs (1955) stated that among anadromous fishes, the earliest arrivals in a particular spawning tributary traveled to the most distant spawning grounds and the later arrivals occupied areas closer to the stream mouth. In the three streams I studied, however, early arrivals did not necessarily ascend to the uppermost spawning areas. Moreover, the sites selected by later arrivals often were located between sites chosen by the earlier spawners.

The female sockeye salmon selects the spawning site, usually near other spawners (Noble, 1938). The presence and stimulation of other spawners may be necessary for successful spawning even though much effort is expended in territorial defense. I seldom saw single spawning pairs but observed rather that fish tended to form more or less isolated groups of several pairs. How much of this behavior is due to preference for certain physical characteristics of the spawning grounds and how much to innate social behavior is not known.

SUMMARY

1. Spawning site selection by sockeye salmon in three small lateral tributaries entering Brooks Lake, Alaska, was studied from 1959 through 1961.

2. Several waves of sockeye salmon spawners ascended the principal study stream in 1959 and 1960 when the numbers of fish were moderate and high but not in 1961, a year of relatively few fish.

3. Both temporal and spatial distribution patterns were defined and found to be relatively constant despite large fluctuations in the number of spawners.

4. The distribution of spawning fish was correlated with stream gradients. Little or no spawning occurred in areas having gradients of less than 0.5% or more than 2.0%.

5. In preferred spawning areas, cobbles from 2.5 to 7.6 cm in diameter made up about 50% of the bottom, materials 1.3 to 2.5 cm about 25%, and particles less than 1.3 cm the remainder.

6. Spawner distribution was more closely related to the composition of the stream bottom than to any other single factor studied.

7. Given two adjacent locations equally desirable with regard to hydrological conditions and bottom composition, sockeye salmon tended to select the site with the most nearby cover and concealment.

8. Early arrivals did not necessarily use the uppermost spawning areas, and later arrivals primarily filled in acceptable areas already in use.

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REDESCRIPTION OF SOME SPECIES OF *CHONE* KRÖYER AND *EUCHONE* MALMGREN, AND THREE NEW SPECIES (SABELLIDAE, POLYCHAETA)[1]

KARL BANSE[2]

ABSTRACT

Generic diagnoses are given for *Chone* (syn. *Megachone*) and *Euchone*. Redescriptions and additions to the descriptions, in part based on study of the types, are provided for some species, *Chone aurantiaca* (new combination), *C. duneri* (syn. *C. bimaculata*), *C. ecaudata* (syn. *C. minuta*), *C. eniwetokensis* (new combination), *C. gracilis*, *C. infundibuliformis* (syn. *C. teres*), *C. magna*, *C. mollis*, *C. paucibranchiata*, *Euchone alicaudata*, *E. analis*, *E. capensis*, *E. elegans*, *E. papillosa*, and *E. rubrocincta*. Three new species, *Chone albocincta*, *Chone veleronis*, and *Euchone velifera* are described. The number of lobes of the collar is rejected for the Sabellidae as a character on the generic level; the diagnostic value of the palmate membrane is discussed.

The sabellid polychaetes are filter feeders which usually live in permanent tubes. Two genera, *Chone* Kröyer and *Euchone* Malmgren, which occur worldwide, are treated here taxonomically. The length of species of *Chone* ranges from 2.5 mm to almost 10 cm, that of species of *Euchone* from a few millimeters to a few centimeters. Some species are quite common on sandy or muddy bottoms (cf. McIntosh, 1916; Hartman, 1944b; Kühlmorgen-Hille, 1963); at least some species are eaten by fishes (McIntosh, 1916; Berkeley and Berkeley, 1954).

The study was initiated because of difficulties in identifying large species of *Chone* in the Synoptic Collection of the Friday Harbor Laboratories, University of Washington. This led to reexaminations of some types and other specimens primarily from the North Pacific and North Atlantic Oceans. The results are an emendation of the generic diagnosis of *Chone*, including the placement of *Megachone* Johnson in *Chone*, the redescription or improvement of the knowledge of some previously known species, and the erection of three new species. Because material of several large species of *Euchone* was at hand, additions to their descriptions are also included, the generic diagnosis is emended, and a new species is described.

Of general taxonomic interest is the discovery of a new species of *Euchone*, *E. velifera*, which has a ventrally deeply incised collar with an additional pair of lateral notches (Figure 12a). A collar that is ventrally moderately incised is known also for *E. papillosa* (Sars) and *E. capensis* Day (Figure 11n). The species otherwise agree fully with the characters of *Euchone*. Similarly, *Chone trilobata* Gallardo has deep lateral notches in its collar but otherwise is typical. Especially the occurrence of bilobed collars in species of *Euchone*, a genus uniquely characterized by the anal depression, provides further evidence in support of Johansson's (1927) strong criticism of the attempt by Bush (1904) to make the collar a character of major importance in distinguishing genera among the Sabellidae. Consequently, genera like *Pseudopotamilla* Bush, separated from *Potamilla* Malmgren only by differences in the collar, should not be maintained. In view of the fact that not all *Euchone* species have a palmate membrane, the question is dis-

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cussed (p. 461) whether the character should be used in the generic diagnosis for the closely related *Chone*.

The observations on some primitive characters in Sabellidae by Banse (1970), especially in regard to the abdominal uncini, are supported by the observations on the species discussed below. To those characters may be added the glandular girdle on the second setiger which is common to all species of *Chone* and *Euchone* and is found also in the sabellid genera *Jasmineira* Langerhans and *Myxicola* Koch. It is considered to be a phylogenetically primitive character not only because of the position of *Chone* and *Euchone* within the family but also because similar girdles occur in other families (e.g., Southern, 1914, for Terebellidae).

METHODS

Because the form of the uncini can vary considerably within the abdomen, the shape of the setae in the anterior abdominal setigers is stressed in the following descriptions. The accessory teeth above the main fang of an uncinus are arranged in several vertical "columns" appearing in side view as horizontal (not strictly so) "rows." The nomenclature for the abdominal segments in *Euchone* follows Banse (1970). The procedure for staining with methyl green introduced by Hofsommer (1913) is described in the same article.

The following abbreviations are used: AHF for Allan Hancock Foundation, University of Southern California, Los Angeles, Calif.; FHL for Friday Harbor Laboratories, University of Washington, Friday Harbor, Wash.; MCZ for Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; NMI for National Museum of Ireland, Dublin; PMNH for Peabody Museum of Natural History, New Haven, Conn.; SMNH for Swedish State Museum of Natural History, Stockholm; SEP for Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Mass.; UCT for University of Cape Town; USNM for U.S. National Museum of Natural History, Washington, D.C.; ZMC for Zoological Museum of the University of Copenhagen; and ZMO for Zoological Museum, University of Oslo. When not noted otherwise, the specimens are in my collection.

SPECIAL PART

CHONE KRÖYER, 1856 EMENDED

CHONE Kröyer, 1856, p. 13.- Sars, 1862, p. 119.- Malmgren, 1866, p. 404.- Langerhans, 1881, p. 111.- Saint-Joseph, 1894, p. 250.- Bush, 1904, p. 189.- Hofsommer, 1913, p. 332.- McIntosh, 1923, p. 287.- Fauvel, 1927, p. 334.- Berkeley and Berkeley, 1952, p. 122.- Ushakov, 1955, p. 417.- Day, 1967, p. 776.
PARACHONIA Kinberg, 1867, p. 355.
MEGACHONE Johnson, 1901, p. 430.
METACHONE Bush, 1904, p. 190, 216.

Type species: *Chone infundibuliformis* Kröyer (cf. Bush, 1904).

Diagnosis: Sabellidae with semicircular branchial lobes united by palmate membrane. Collar conspicuous. Postsetal girdle of glands on second setiger. Ventral shields sometimes present. Ends of abdomen of typical sabellid form. Three types of thoracic notosetae: upper, anterior ones limbate, sometimes in two series of different length; lower, anterior ones narrowly limbate (bayonet-type); and lower, posterior ones spatulate or subspatulate. Thoracic neuropodial uncini long-handled, acicular. Abdominal notopodial uncini avicular, with square or rounded bases; abdominal neurosetae limbate.

Remarks: The emended diagnosis comprises the same species as previously (cf. Hartman, 1959, 1965, and below), although it contains as new characters the postsetal girdle of glands, the ventral shields, the bayonet-like setae, and the qualification "or subspatulate setae." The usual occurrence of ventral nude filaments in the branchial crown, the occasional presence of otocysts, and the diagnostic characters pertaining to the family are omitted. There are usually eight thoracic setigers; very rarely a specimen deviates from this number.

Parachonia has been included in *Chone* by Johannson (1927), *Metachone* by Fauvel (1927; see also Hartman, 1942b).

The type species of *Megachone* Johnson, *M. aurantiaca*, is redescribed below, based in part on the holotype. Contrary to the statement by Johnson (1901), the species does have ordinary spatulate setae in the thoracic notopodia and thus agrees in every respect with *Chone*.

The diagnosis as given has one weakness: The original reason of Kröyer (1856) in creating *Chone* was the funnel-like appearance of the lophophores, or branchial crown, caused by the palmate membrane. This membrane is not of so unique value as a generic character as originally thought. Sars (1862) was the first to point out that the membrane occurs also in other genera. More important is that it may be present or absent in the closely related *Euchone* (Banse, 1970). If the palmate membrane were considered also in *Chone* as a specific character, *Dialychone* Claparède would become a synonym of *Chone* (cf. Fauvel, 1927). For the practical need of identification, however, considerable difficulties would result. For example, a large species of *Oriopsis* Caullery and Mesnil (cf. *O. rivularis* Annenkova, with bayonet-type thoracic notosetae) would externally be distinguishable from *Chone* only by the absence of the postsetal glandular girdle on the second setiger. Anatomically, *Oriopsis* would, of course, be quite different because it belongs to the thoracogoneate Fabriciinae (Zenkevitch, 1925) with their unique gonoducts. Because eggs may occur in thoracic segments also in abdominogoneate sabellids (cf. *Euchone hancocki* Banse), identification without anatomical study may sometimes not be possible. In view of these problems it seems wise to define *Chone* as above until intensive anatomical studies of representatives of the various subgroups of Fabriciinae have been made. These may yield a more natural and hence more convincing system than is available now.

Among most species of *Chone*, the collar has a very narrow dorsal gap. *C. trilobata* has a collar with deep lateral notches. The bayonet-type setae (also called basal or geniculate setae) were described in some species by previous authors (cf. Fauvel, 1927; Eliason, 1962) but seem to be present in all members of the genus. The lower posterior thoracic notosetae are sometimes subspatulate, as in *C. filicaudata* Southern and *C. eniwetokensis* (Reish).

The abdominal uncini with square bases and few teeth, thought to be typical for *Chone* (cf. Figure 1k) are found in many species only in anterior abdominal segments, as is the case also in *Euchone* (Banse, 1970). The uncini of posterior setigers can have instead small rounded bases and a high crown of accessory teeth (cf. Figure 6i). Such uncini occur similarly in other genera of Sabellidae and in related families and are thus phylogenetically more primitive than the typical hooks of *Chone*. Further, they can be present in the same tori together with typical ones, as in *C. ecaudata* Moore and *C. albocincta* new species (cf. *Euchone elegans*). Their position shows that ontogenetically they have been formed first. Also this points to the primitiveness of the posterior uncini. Likewise Okuda (1946) has shown in a developmental study of ?*C. ecaudata* (see below) that the abdominal uncini first formed are of the primitive type and similar to those found, for example, in *Oriopsis;* initially they occur even in the thorax.

In spite of the clarification of diagnostic characters, very little can yet be said about the relations among species of *Chone*. Certainly, species with ventral shields are more primitive than those with fully glandularized epidermes because reasonably primitive Sabellidae should have shields. Significantly, the typical abdominal uncini with square bases seem to be present throughout the abdomen only among *Chone* species having a fully glandularized epidermis (possibly also in *C. eniwetokensis*, according to Reish, 1968).

CHONE INFUNDIBULIFORMIS KRÖYER

Figure 1

CHONE INFUNDIBULIFORMIS Kröyer, 1856, p. 33.- Malmgren, 1866, p. 404; 1867, p. 214.- Hofsommer, 1913, p. 332.- McIntosh, 1916, p. 35, 39.- Imajima, 1961, p. 98.- Hartmann-Schröder, 1971, p. 520. See also p. 465.

CHONE TERES Bush, 1904, p. 215.- Hartman, 1942b, p. 87; 1959, p. 539.

not *CHONE TERES*.- Okuda, 1934, p. 236; 1946, p. 171.- Imajima and Hartman, 1964, p. 365 (for these three references see *C. ecaudata*).- Chlebovich, 1961, p. 231 (see Remarks).

Diagnosis: A large *Chone* species without ventral shields. Branchial basis as long as level collar. About 20 pairs of radioles, connected for two-thirds to three-fourths of length by palmate membrane, with free ends very short and broad. First bundle of setae of normal size, inserted more dorsally than following notosetae.

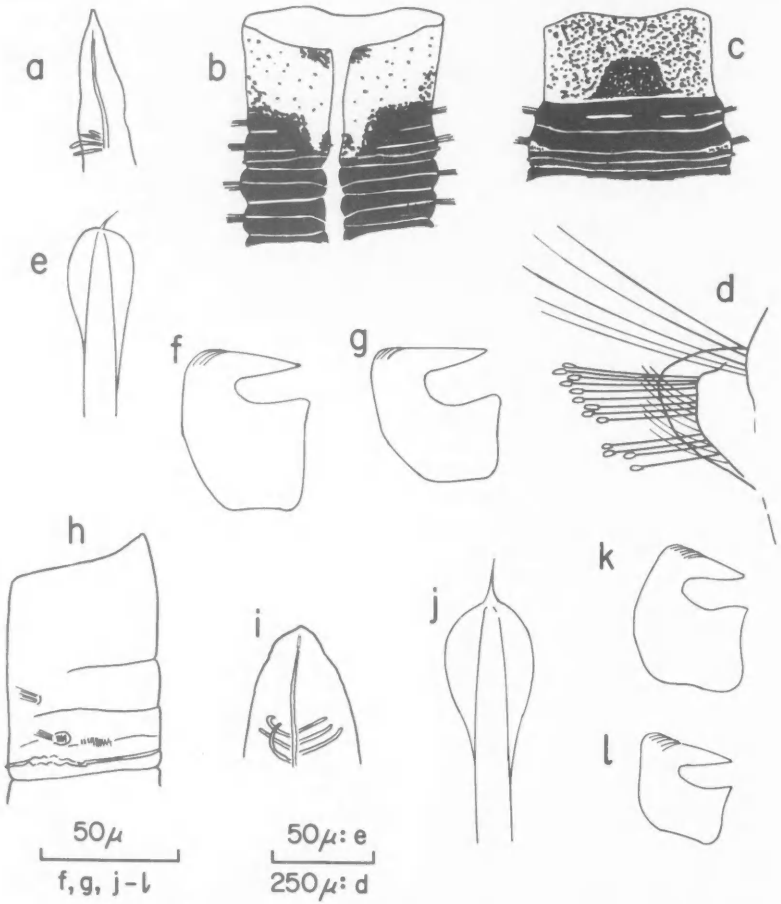

FIGURE 1.—*Chone infundibuliformis*; a from Godhavn; b-g from Egedesminde; h-l from holotype of *C. teres*: a, end of dorso-median radiole; b, c, dorsal and ventral staining pattern of anterior end of trunk; d, anterior view of third thoracic notopodium. Setae schematic, most upper limbate setae omitted from this segment; f, g, uncini from third and approximately 45th abdominal setigers; h, slightly schematic side view of anterior end, branchial crown omitted; i, end of fully developed radiole; j, spatulate seta from sixth setiger; k, l, abdominal uncini from third and approximately 70th abdominal setigers.

Broad notopodial lips in thorax. Spatulate setae with pointed tips. Abdominal uncini uniform, with straight crests; small crowns with some small teeth in several columns; rostra not extending beyond bases.

Material studied: Egedesminde and Godhavn, west coast of Greenland (SMNH 6861; 6862), and Safehavn and Hornsund, Spitsbergen (SMNH 6863; 6864 in part). The material of Malmgren (1866), 8 specimens.

Greenland, locality unknown. Collected by C. Lütken in the last century, USNM 372, 2 specimens.

Dutch Harbor, Alaska, holotype of *Chone teres*. PMNH 2761 (previous number: 5-2).

Additions to the Description: Since the type material from "the Greenlandic sea" is lost (letter by Dr. J. B. Kirkegaard, ZMC, 27 Feb. 1970), excellently preserved Arctic specimens of Malmgren (1866) are used for additions to the description of the species. The features of the especially suitable specimen from Egedesminde are stressed on the assumption that Kröyer's material was collected also off the west coast of Greenland where most of the traffic went during that time.

The trunks of the smallest specimens are a little less than 2 cm long, are about 1 mm wide, and have about 50 abdominal segments. Large specimens have 70 to 80 abdominal segments and are, when fixed in their tubes, up to 6 or 7 cm long (total) and about 3 mm wide. About 1½ cm of the length of the large animals is contributed by the branchial crown. The radioles number up to 15 or 16 pairs (up to 22 according to Kröyer, 1856). In addition to the radioles, about half a dozen pairs of inconspicuous nude ventral filaments are present; the longest ones are almost a fifth of the length of the branchial crown. The palmate membrane extends to two-thirds or three-quarters of the length of the radioles and continues as broad flanges on the radioles. The ends of the radioles are broad and short (Figure 1a); however, the most ventral pinnated radioles have relatively longer nude tips which are twice as long as shown in the figure and sometimes have an additional short filiform end.

The collar extends dorsally to the end of the second setiger (Figure 1b). Thus the furrow separating the first and second setigers does not reach the fecal groove. This character is easily made out. On the ventral side (Figure 1c), the first (buccal) segment is not distinctly separated from the collar in unstained animals. The body is essentially rounded and entirely covered by glandular tissue, i.e., no ventral shields are present. The glandularization is conspicuous even in unstained specimens. The segments appear as biannulate in the thorax and through the 40th to 50th abdominal setiger which is most of the abdomen, by length. Dorsally in the thorax after the second setiger, the intrasegmental furrows bend posteriorly before joining the fecal groove. This seems characteristic for the species; Hofsommer (1913), however, stated that the furrows bend forward. The postsetal glandular ring on the second setiger, usually appearing in *C. infundibuliformis* as a sunken fine line, is present (contrary to Ushakov, 1955).

The first bundle of thoracic setae originates slightly dorsad to the level of the notosetae of the following segments. In these segments notopodial lips are conspicuous (Figure 1d) when not withdrawn. Limbate and spatulate thoracic setae were figured by Malmgren (1866, Plate 28, Figure 87B, B^1, B^2). Whereas Malmgren depicted spatulate setae with and without pointed tips, I have found only setae with pointed tips (Figure 1e; animals from the four localities of Malmgren's material); these, of course, are often broken off. In the juvenile specimens, the tips are relatively twice as long as shown here. Bayonet-type setae have already been observed by Fauvel (1927) for the species. The thoracic uncini are arranged in irregular double rows except in juveniles; therefore, the oldest (i.e., the dorsal) upper parts of the tori of the adults have only single rows. The abdominal uncini have beaks which do not extend beyond the bases of the uncini (Figures 1f and 1g; checked also at 80th setiger, about 10 segments before the pygidium). The tips of the accessory teeth lie on the continuation of the rostra. In the anterior segments, these teeth seem to be of uniform size,

whereas posteriorly one larger accessory tooth can sometimes be distinguished. Several columns of teeth are present both anteriorly and posteriorly. The long and short limbate abdominal neurosetae are much finer posteriorly than anteriorly.

When treated with methyl green, the thorax and the anterior part of the abdomen stain uniformly. This holds also for the first segment which is visible only ventrally (Figure 1c). The collar shows a variable pattern, not related to locality or size of specimens. It can be either almost fully stained—nearly as intensive as the trunk—or be almost devoid of stain-accepting cells so that the anterior border of the first setiger is indicated only by a midventral white line. The intrasegmental furrow on the first setiger can be weakly indicated or not visible. Stain-accepting cells (and hence, presumably, the glandularization of the body surface) are not fully developed in juveniles. The cells are present in conspicuous concentrations only along the inter- and intrasegmental furrows leaving free areas between them, especially dorsally in the thorax.

The holotype of *Chone teres* was inspected, and the following additions to the description may be made; slight differences from typical *C. infundibuliformis* will be pointed out. The common base of the branchiae is hidden below in the collar which is relatively large (Figure 1h). The collar ends dorsally at the posterior border of the second setiger. The radioles are of unequal length, as if some were regenerating. The longest ones have very broad ends (Figure 1i). Segments are clearly biannulate through approximately the 35th abdominal segment; posterior to this region, staining helps to recognize the intrasegmental furrows. The anterior border of the first setiger is visible only ventrally and laterally (Figure 1h). The intrasegmental furrow of this segment is indicated merely by yellowish color after staining of the animal with methyl green. The anterior border and the intrasegmental furrow of the second setiger do not reach the fecal groove. The glandular girdle is irregularly broadened laterally. On the following thoracic segments, the intrasegmental furrows bend rearward dorsad of the notosetae and the intersegmental furrows bend forward before joining the fecal groove.

The setal bundle of the first setiger is only slightly smaller than those of the following segments but is situated in a slightly more dorsal position than that of the second setiger. As already stated by Bush (1904), geniculate setae are present in the remaining segments; the spatulate setae have pointed tips (Figure 1j). Thoracic uncini are arranged in irregular double rows in some parapodia. Abdominal uncini are nearly identical anteriorly and posteriorly (Figures 1k and 1l). Their crests are almost straight (less so posteriorly). Several rows of small accessory teeth are arranged in several columns. The rostra do not surpass the bases of the uncini; the cavities below the rostra are not rounded in side view as in Greenlandic, *C. infundibuliformis* (Figure 1f).

Upon staining, the thorax does not accept the dye dorsally as readily as laterally and ventrally; similarly, the ventral epidermis of the abdomen retains the dye longer than that of the dorsal side. In the abdomen the tissues along the inter- and intrasegmental furrows stain more strongly than the fields between them so that most segments appear to bear three whitish rings rather than one, the intrasegmental furrow. Yet, I have the impression that the epidermis is fully glandularized.

Remarks: *Chone teres* is considered a synonym of *C. infundibuliformis* although the abdominal uncini are slightly different and the ventral side in *C. teres* accepts stain relatively more than the dorsal side. Noteworthy is the shortness of the branchial crown which contributes approximately one-fifth of total length in Greenlandic specimens preserved in their tubes, but one-eighth in *C. teres*. All other specific characters agree. When more material from Alaska becomes available, special attention should be paid to the mentioned deviating characters to check the justification of placing *C. teres* in synonymy.

The record of *C. teres* by Chlebovich (1961) is not included among the synonyms of *C. infundibuliformis* because he lists *C. cincta* Zachs, as described by Ushakov (1955), among his

synonyms. The figure of the tips of the radioles of *C. cincta* by Ushakov (1955, Figure 159 K) clearly shows a feature very different from *C. infundibuliformis;* it may be noted that Zachs (1933), while describing *C. cincta*, observed that the gills are like those of *C. infundibuliformis.*

The number of records for the long-known *C. infundibuliformis* is very large. Lists by McIntosh (1923), Pettibone (1954), and Hartman (1969) may be consulted, but it must be noted that most of the records cannot be evaluated under the viewpoints presented here without the specimens of the various authors. Therefore, the list of synonyms on p. 461 has been kept short.

Regarding the distribution and synonymy of *C. infundibuliformis* in the North Atlantic, McIntosh (1916) was the first to emphasize the difference between the abdominal uncini of Greenlandic specimens (very small accessory teeth, forming a straight line with the rostrum, cf. Figure 1f) and those of southern forms (teeth coarse, their tips lying on a convex line above the continuation of the rostrum similar to Figure 3g), thus implying that different forms are involved. Most European records of *C. infundibuliformis* will not be identifiable without the authentic material of the several species; confusion is possible with *C. fauveli*, *C. normani*, and *C. reayi*, all described by McIntosh, and *C. ungavana* Chamberlin. Fauvel (1927, p. 346) has already suggested that *C. reayi* may belong to *Jasmineira* Langerhans.

From the description alone, it is certain that most, if not all, of the material of Fauvel (1913, 1914) is not *C. infundibuliformis.* McIntosh (1916) even believed that Fauvel had before him *C. duneri*, which is very diffierent from any of the species listed in the previous paragraph. All of Fauvel's drawings of abdominal uncini show coarse accessory teeth not found in *C. infundibuliformis* from Greenland. Also, Fauvel (1913) stated that the teeth in some specimens were arranged in one row only. Fauvel emphasized the variability within specimens of the abdominal uncini (as well as of the tips of the spatulate setae) for his material. The shape of abdominal uncini, however, does not vary in *C. infundibuliformis.* Similarly, Lukasch (1911, Plate 2, Figures 7 and 8) shows a conspicuous divergence of the form of the anterior and posterior abdominal uncini in material from the Kola Fjord; as shown, this does not occur in Greenlandic material. Also, drawings in Fauvel (1927) do not refer to typical *C. infundibuliformis.* Further, Hartman's (1944b, Plate 23, Figure 46) figure of an uncinus of *C. infundibuliformis* from the Swedish west coast resembles that of *C. fauveli*; according to Eliason (1962, see his remarks under *C. duneri*), true *C. infundibuliformis* is not found on that coast. Finally, uncini vaguely similar to those of *C. fauveli* have been drawn by Rioja and Lo Bianco (1931) for Iberic material identified as *C. infundibuliformis*, so that this record too is uncertain.

CHONE PAUCIBRANCHIATA (KRÖYER)

SABELLA PAUCIBRANCHIATA Kröyer, 1856, p. 22.

Material studied: Holotype, from Finmark, northern Norway (from label). ZMC.

The original description was based on a single specimen. The species has been regarded since Malmgren (1866) as a junior synonym of *Chone infundibuliformis* Kröyer. However, the holotype has ventral shields whereas *C. infundibuliformis* does not. The shields are especially visible after using methyl green; the thorax laterally does not stain. The synonymy of this old species cannot be given without a thorough redescription of other European forms: possibly, the species is indeterminable.

The mature specimen, with polygonal eggs of about 50 μ diameter, is small, having a trunk length of about 10 mm to which the branchial crown adds about 3.5 mm. The greatest width is slightly less than 1 mm. Approximately 45 abdominal setigers are present. As observed by Kröyer (1856), the animal has three pairs of branchia and some short nude filaments. The length of the palmate membrane, which is now torn, extended at least to one-third of that of the branchial crown but not more than two-thirds. The thoracic uncini are long-handled. The first bundle of setae originates slightly more dorsally than the notosetae of the second setiger,

but all limbate setae are broken off so that a complete redescription of *C. paucibranchiata* is not possible.

CHONE DUNERI MALMGREN

Figure 2a, b

CHONE DUNERI Malmgren, 1867, p. 225.- Hofsommer, 1913, p. 336.- Pettibone, 1954, p. 339.- Hartmann-Schröder, 1971, p. 517.

CHONE sp. I Banse, Hobson, and Nichols, 1968, p. 547.

CHONE BIMACULATA Banse and Nichols, 1968, p. 227.- Nichols, 1968, p. 61.

not *CHONE DUNERI*.- Pettibone, 1956, p. 577 (a *Euchone* sp., see Remarks).

Diagnosis: A *Chone* of intermediate size without ventral shields. Branchial basis somewhat higher than oblique collar. Up to about 10 pairs of radioles, connected for about two-thirds of length by palmate membrane, with narrow, very long free ends. First bundle of setae very small. Conspicuous notopodial lips in thorax. Spatulate setae with pointed tips. Abdominal uncini with broad bases and small accessory teeth.

Material studied: Point Barrow, northern Alaska, 5 miles offshore, 89 m, 6 Oct. 1949. Collected by G. E. McGinitie, identified by M. H. Pettibone (Pettibone, 1954). USNM 23633, 2 specimens.

Paratypes of *C. bimaculata*, from station 5 of Lie (1968, 3 May 1963). USNM 36280, 4 specimens.

West Sound, Orcas Island, Wash., approx. lat 48°36′N, long 112°57′W, 40 m, mud, July 1967. Collected by H. L. Sanders. 1 specimen. Unpublished record.

Additions to the Description: The longest complete specimens at hand, from Point Barrow, are 18 and 26 mm long. In all animals examined, the free ends of the radioles are one-quarter to one-third as long as the entire radioles, tending to be relatively longest on the dorsal side of the branchial crown. Ventrally, about four pairs of nude filaments are found; two pairs are almost as long as the branchial crown and at least some have cartilaginous axes. As described by Malmgren (1867, Plate 14, Figure 75), the collar barely conceals the peristomium so that the branchial base is fully visible. The first (buccal) segment is not clearly distinguishable from the collar in unstained animals. A postsetal girdle of glands is present on the second setiger. Ventral shields are absent. The first fascicle of setae is very small in comparison with the following ones. From the second setiger on, notopodial lips are conspicuous. The thoracic neurosetae are winged hooks in Arctic and Puget Sound specimens (see Banse and Nichols, 1968, Figure 2g). An anterior abdominal uncinus is shown in Figure 2a.

The staining pattern of the specimens from Point Barrow (Figure 2b) is similar to that described by Hofsommer (1913) for an animal from the North Sea. In contrast to the appearance in species with ventral shields, the intensity and appearance of stained tissue in *C. duneri* is uniform around the entire circumference of the thorax and anterior abdomen. Ventrally, the small, weakly dyed fields in the presetal and postsetal rings are present also in the first abdominal setigers but disappear gradually by about the tenth abdominal segment. The dorsal pattern is characterized as follows: The median folds of the collar remain white. The unstained rings in the plane of the parapodia bend rearward on the dorsal surface similarly to but less pronounced than in *C. infundibuliformis* (Figure 1b). Weakly stained fields are present within the presetal stained rings of the thorax (cf. Hofsommer, 1913, text figure h); they extend laterally on the abdomen to the level of the neuropodia. Consequently the presetal rings of the anterior abdomen are nearly split in two. Occasionally, the postsetal rings are equally split but this is a condition which may occur also in other species without it having been noted herein. In most of the specimens from Washington which are smaller and in part not as well preserved, the pattern agrees but in some the dark longitudinal midventral strip is less conspicuous than in Figure 2b.

Remarks: Earlier authors have apparently not noted the glandular ring on the second tho-

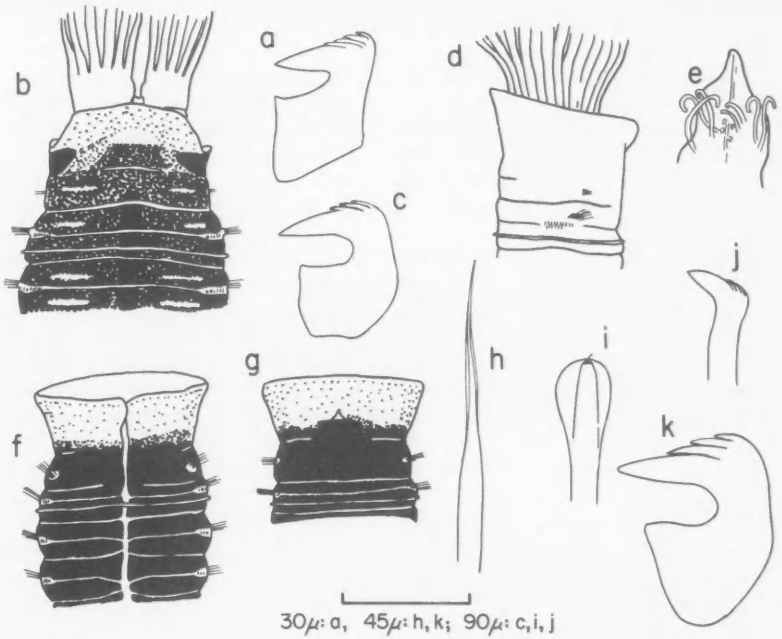

FIGURE 2.—*Chone duneri*, from Point Barrow: a, middle uncinus from fourth abdominal setiger; b, ventral view of anterior end of thorax after staining; *C. aurantiaca*; c from holotype, others from USNM 43637: c, uncinus from second abdominal setiger; d, anterior end from the right side; e, end of median radiole, somewhat schematic; f, g, anterior end in dorsal and ventral views after staining. Slightly schematic, branchial crown omitted; h, i, bayonet and spatulate setae from sixth setiger; j, uncinus from fourth setiger; k, uncinus from approximately 60th (12th to last) abdominal setiger.

racic setiger; Ushakov (1955) has specifically stated that it is absent. This character was one of the main reasons for describing *C. bimaculata;* at that time it was not realized that all *Chone* species have such a ring. Contrary to the original description, the intersegmental furrows of the paratype do not stain and the thoracic intrasegmental furrows, in the plane of the parapodia, are ventrally interrupted by the strongly stained longitudinal midventral line (cf. Banse and Nichols, 1968, Figure 2j). Thus, there is no justification for maintaining *C. bimaculata.*

The record of *C. duneri* from Labrador (Pettibone, 1956, USNM 23635, 2 specimens) is a *Euchone* sp. with conspicuous ventral shields.

CHONE AURANTIACA (JOHNSON)

Figure 2c-k

MEGACHONE AURANTIACA Johnson, 1901, p. 430.- Hartman, 1938, p. 19; 1959, p. 549.

Diagnosis: A large *Chone* species without ventral shields. Branchal basis shorter than the slightly oblique collar. About 25 pairs of radioles connected for four-fifths of length by palmate membrane, with free ends short and tapered. First bundle of setae small, inserted at same level as following notosetae. Spatulate setae without pointed tips. Abdominal uncini uniform, with a few columns of three to four coarse

accessory teeth each; rostra extending beyond bases. With caudal appendix?

Material studied: Holotype, from Port Orchard, Wash. MCZ 1933.

Near Friday Harbor, Wash., lat 48°31.7'N, long 122°58.0'W, at the 0-ft level, in shell gravel, 6 July 1953. Collected and identified as *C. infundibuliformis* by R. I. Smith. FHL 1700, 1 specimen. Unpublished record.

From same site, presumably intertidal, in fine gravel, 10 July 1968. Collected by S. Heller. USNM 43637, 1 specimen. Unpublished record.

Redescription: The holotype is now very poorly preserved; it apparently had been allowed to become dry. The diagnostic characters, i.e., the position of the setae on the first setiger, the form of the spatulate setae (in one notopodium), and the abdominal uncini (Figure 2c) can still be recognized; the collar has been depicted by Johnson (1901, Plate 18, Figure 186). According to Johnson, the trunk had 75 setigers and was 87 mm long.

The following description is based on the two animals from near Friday Harbor which are complete, fixed outside their tubes, and well preserved. One specimen (USNM) has 8 thoracic and almost 70 abdominal setigers. The length of the branchial crown is approximately 10 mm, that of the trunk roughly 60 mm, and the greatest width is about 3 mm. The other animal (FHL) has approximately 60 abdominal setigers, its trunk length is about 60 mm, the greatest width almost 5 mm, and the branchial crown approaches 15 mm in length.

In the preserved material the branchial crown forms a funnel with reflexed upper margin, as common in the genus. The basis of the crown is hidden by the collar (Figure 2d). The number of radioles is 20 pairs (USNM) and 26 pairs (FHL). They are united by a palmate membrane for about four-fifths of their length. The tips of the radioles extend beyond the origin of the distal pinnules; they are short and broad, tapering at the ends (Figure 2e). Ventrally the tips are slimmer, dorsally a little wider than shown. Many pinnules reach almost to the ends of the radioles. As nude filaments were not found, they must be very short. The palps are small triangular processes.

The collar is slightly oblique, being a little longer ventrally than dorsally. It extends dorsally to the intrasegmental furrow of the second setiger (Figure 2f). Consequently, the posterior border of the first setiger does not end in the fecal groove. Ventrally, the first (buccal) segment is not clearly set off from the collar. Ventral shields are not present, and the entire epidermis is glandularized. Setigers in the thorax and abdomen are biannulate. The intrasegmental division of the first setiger is poorly discernible and has not been drawn in Figure 2g. The dorsal pattern of the inter- and intrasegmental borders in the thorax is shown in Figure 2f. The pygidium is pointed. A damaged filiform appendage was seen in one specimen (USNM). It appears to be similar to the caudal appendage of *C. filicaudata* Southern. It is absent in the other animal (FHL).

The first setiger has bundles of a few short setae which insert at right angles to the notosetae of the following segments but on the same level (Figure 2d). Each of the remaining thoracic notopodia has almost 2 doz of upper limbate setae in two sizes and below an anterior series of bayonet-type setae (Figure 2h) with shafts almost as thick as the posterior series of spatulate setae; the bayonet-type setae taper abruptly at about the level of the body surface. The spatulate setae (Figure 2i), 1½ to 2 doz per parapodium, are without pointed tips but some have very tiny hairs instead. The distal end of such a seta can appear as having a dimple. These spatulate setae are present also in the holotype, but were overlooked by Johnson (1901).

About 3 doz of neuropodial hooks (Figure 2j) are arranged in irregular double rows in most thoracic neuropodia. The uppermost half dozen or so are in single rows. The abdominal uncini (Figure 2k) are uniform in shape anteriorly and posteriorly. When seen from the side, they have three or four large coarse accessory teeth arranged in three or four columns. The rostra extend beyond the bases. Two dozen uncini are present even in the 50th to 60th setigers.

Some irregular orange-red speckles remain on the collar and anterior segments of the holotype

which was preserved in Formalin and stored in alcohol. The second specimen was orange-red in life as was the holotype while freshly preserved (Johnson, 1901). Upon staining with methyl green the entire body surface turns uniformly green except for the collar and the inter- and intrasegmental furrows.

Remarks: Because of the presence of spatulate setae in the type species, *Megachone* is a synonym of *Chone* (cf. p. 461).

Megachone aurantiaca may be distinguished from the similar species, *C. infundibuliformis*, by the insertion of the first thoracic bundle of setae and the form of the abdominal uncini. *Chone magna*, when deprived of the branchial crown, will also be difficult to distinguish from *C. aurantiaca* but can be recognized by the same diagnostic characters. *Chone mollis*, the third fairly large species of *Chone* on the North American west coast, has a different arrangement of intersegmental furrows anteriorly (Figure 3c), large notopodial lips and somewhat different abdominal uncini, especially posteriorly (Figure 3h).

CHONE MOLLIS (BUSH)

Figure 3

METACHONE MOLLIS Bush, 1904, p. 216.
CHONE MOLLIS.- Hartman, 1942b, p. 87; 1944b, p. 279; 1969, p. 673.

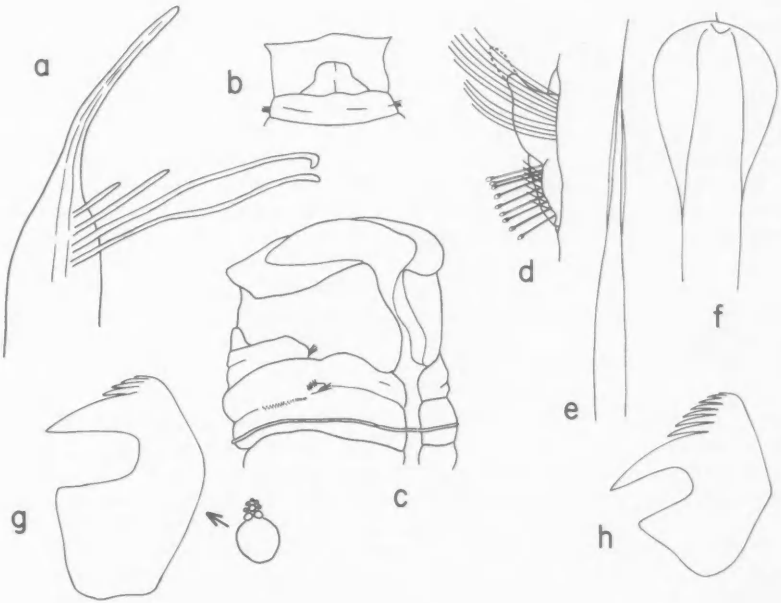

FIGURE 3.—*Chone mollis*; AHF 003258, setae not drawn to scale: a, end of median radiole, pinnules schematically drawn for one side; b, ventral view of anterior end. Somewhat schematic, branchial crown omitted; c, anterior end from the right side, branchial crown omitted; d, anterior view of thoracic notopodium. In dotted outline the extended cirrus; e, bayonet-type seta; f, spatulate seta; g, uncinus from second abdominal setiger. Detail: top viewed *en face;* h, uncinus from 30th abdominal setiger (of about 40 total abdominal segments).

Diagnosis: A large *Chone* species without ventral shields. Branchial basis hidden by level collar. Approximately 15 pairs of radioles connected for two-thirds of length by palmate membrane, with free filiform ends of intermediate length. First bundle of setae small, inserted in a furrow (continuation of anterior border of first setiger) on same level as following notosetae. Conspicuous notocirri and notopodial lips in thorax. Spatulate setae without pointed tips. Anterior abdominal uncini with rostra about as long as bases, few coarse teeth in two columns; crowns somewhat enlarged in posterior segments.

Material studied: Tomales Bay, Calif., near the low tide line. Summer 1941. Collected by F. A. Pitelka; identified by O. Hartman. AHF n 424, 2 specimens.

Tomales Bay, Calif., clam flats. 8 June 1941. Collected by S. F. Light; identified by O. Hartman. AHF 003258, 2 specimens.

Off Long Beach, Calif., *Velero* station 4886, lat 32°42′34″N, long 118°08′15″W, 22 Feb. 1957. AHF 003218, 6 specimens.

Inner Tomales Bay, Calif., across from the village of Marconi. Coarse intertidal sand. Collected and identified by J. S. Tucker. 6 specimens.

Additions to the Description: The largest animals (AHF 003258) are up to 5 cm long (total) and 3 mm wide. The ends of their radioles have flanges (Figure 3a) that taper fairly abruptly at the level of the last pinnules. In specimens from Tomales Bay of 3-cm length and 2-mm width, the free ends may be almost twice as long as shown in the figure. The largest of the several ventral nude filaments recognizable in the latter specimens reach two-thirds of the length of the branchial crown.

The anterior end is distinguished ventrally by a very prominent first (buccal) segment (Figure 3b) that is clearly set off from the collar and tends to be split longitudinally. The anterior border of the first setiger is complete; laterally, it converges with the anterior border of the second setiger where the first bundle of setae inserts (Figure 3c). The furrow between the first and the second setiger extends to the fecal groove. The segments may appear as biannulate at least through the 25th abdominal setiger.

The thoracic notopodia (Figure 3d) have massive lips. The posterior lips bear more or less contracted notocirri. The whole structure may be almost completely withdrawn into the surrounding epidermal pocket so that only the contracted cirrus, resembling a papilla, is visible under favorable illumination. The bayonet-type setae (Figure 3e) arise from the anterior lower lip shown in Figure 3d. The diameter of their shafts is three-fourths the width of the spatulate setae. They taper abruptly at about the level of the body surface. Spatulate setae (described by Hartman, 1944b, as having a dimple) sometimes have very minute tips (Figure 3f) which presumably are usually broken off. Thoracic uncini may or may not be arranged in irregular double rows. The anterior abdominal uncini (Figure 3g; cf. Bush, 1904, Plate 35, Figure 28; Hartman, 1942b, Figure 141; 1944b, Plate 23, Figure 49) have small and few teeth, in two columns. Posteriorly, however, the number of rows increases (Figure 3h) as well as the number of columns.

In stained specimens, the entire epidermis is uniformly green, i.e., ventral shields are absent. A white crescent-shaped area is found ventrally on the collar anterior to the first segment. The intrasegmental furrows, dorsally in the thorax, are inclined rearwards as in *C. magna* (cf. Figure 5e).

CHONE GRACILIS MOORE

Figure 4

CHONE GRACILIS Moore, 1906, p. 257.- ?Hartman, 1961, p. 42; 1969, p. 665 (same record).
not *CHONE GRACILIS* Moore.- Berkeley and Berkeley, 1932, p. 315; 1942, p. 206; 1952, p. 123, in part (for all, see *C. ecaudata*).
not *CHONE GRACILIS* Hofsommer, 1913, p. 342 (homonym).
CHONE INFUNDIBULIFORMIS.- Pettibone, 1954, p. 378, in part.

Diagnosis: A *Chone* species of intermediate size without ventral shields. Ten pairs of ra-

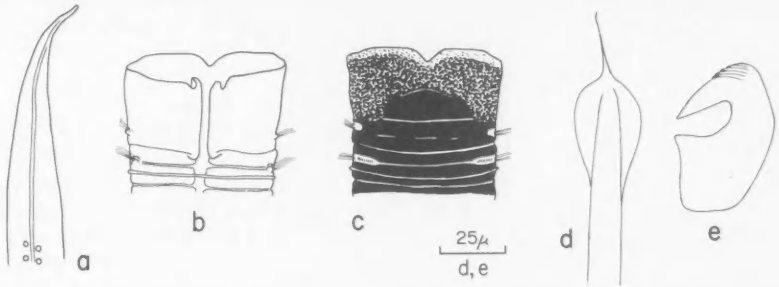

FIGURE 4.—*Chone gracilis*, from holotype: a, end of median radiole. Origin of pinnules indicated schematically; b, dorsal view of anterior end, branchial crown omitted; c, ventral staining pattern of anterior end of trunk; d, spatulate seta from sixth setiger; e, uncinus from third abdominal setiger.

dioles connected for three-fifths of length by palmate membrane, with free ends gradually tapering to pointed tips. Branchial basis as high as collar; collar almost level, with distinct ventral indentation. First bundle of setae of normal size, inserted at same level as following notosetae. Rounded notopodial lips in thorax. Spatulate setae with long pointed tips. Abdominal uncini uniform, with small accessory teeth in several columns; rostra not extended beyond bases.

Material studied: Holotype, from Kodiak Island (originally spelled Kadiak), southwestern Alaska. USNM 5513.

Additions to the Description: The original description of the specimen, a mature female, was rather complete but was accompanied only by a few figures so that there has been some confusion with other species. The branchial basis is as high as the collar. A tip of a median (lateral) radiole is shown in Figure 4a. The collar (Figures 4b and 4c) inserts dorsally on the anterior part of the second setiger. The free dorsal edge of the collar is folded inwards as stated by Moore (1906). The edge rises ventrolaterally and ventrally slightly over the height attained dorsally. A midventral indentation of the collar is very conspicuous. The first (buccal) segment is distinct ventrally even without staining. The intrasegmental furrow on the second setiger reaches the fecal furrow. A postsetal girdle of glands is present on this setiger. The first bundle of setae, now preserved on only one side, is of ordinary relative size and inserts at the same level as the notopodia of the following segments. Moore (1906, Plate 12, Figure 62) depicted bayonet-type setae without designating them as such. The spatulate setae (Figure 4d) have unusually long tips as shown also by Moore (1906, Plate 12, Figure 64). The abdominal uncini (Figure 4e) are uniform throughout and have about six rows of approximately six small teeth which are difficult to count. Upon staining with methyl green, thorax and most of the abdomen turn uniformly green excepting the intersegmental and intrasegmental furrows; also, the presetal parts of the segments dorsal in the thorax are paler than the postsetal parts. Ventrally, the incomplete anterior and posterior borders of the first segment are distinct. The intrasegmental furrow of the first setigerous segment is poorly visible.

Remarks: I concur with Moore (1906) that this is a species of its own; it is distinct from *C. infundibuliformis* (contrary to Pettibone 1954). Based on his description and the observations provided here, *C. gracilis* is distinguished among the species with glandularized epidermis by its ventrally indented collar; another diagnostic character is the combination of a relatively long branchial crown which contributes more

than one-third of the total length, with the form of the tips of the radioles and spatulate setae, the insertion of the collar dorsal on the second setiger, and the form of the abdominal uncini.

The species is definitely known from southwestern Alaska. Hartman (1961, 1969) recorded it from California but referred expressly to the description by Berkeley and Berkeley (1952). As this largely represents *C. ecaudata* (see p. 473), the record needs confirmation.

CHONE MAGNA (MOORE)

Figure 5

EUCHONE MAGNA Moore, 1923, p. 245.- Hartman, 1961, p. 42.

CHONE MAGNA.- Hartman, 1969, p. 669.

Diagnosis: A large *Chone* species without ventral shields. Branchial basis shorter than oblique collar. About 30 pairs of radioles, connected for two-thirds of their length by palmate membrane, with free ends narrow and very long. First bundle of thoracic setae small, inserted slightly ventrad to following notsetae. Spatulate seta without pointed tips. Abdominal uncini uniform, with three of four coarse accessory teeth in two columns; rostra extending beyond bases.

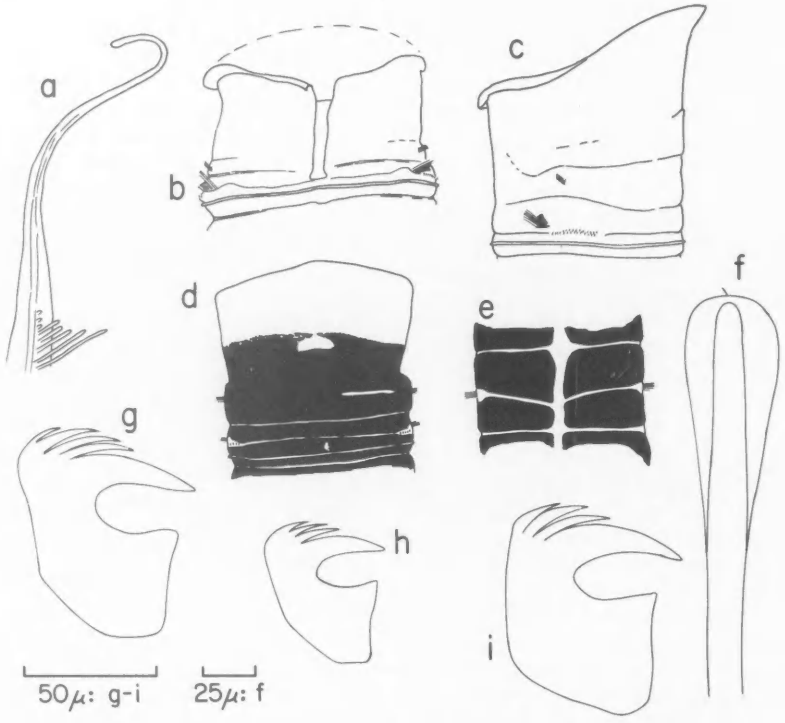

FIGURE 5.—*Chone magna*; e, g, and h from holotype, the others from animals from Washington: a, end of radiole; b, c, ventral and side views of anterior end, branchial crown omitted, setae schematic; d, ventral view of anterior end of stained specimen, body outline schematic; e, dorsal view of posterior thoracic segment of stained specimen; f, spatulate seta; g, h, uncini from 30th and approximately 70th (last of fragment) abdominal segments; i, uncinus from 70th (10th before last) abdominal segments from other animal.

Material studied: Holotype, from almost 500-m depth off California. USNM 17281.

North of Santa Catalina Island, Calif., *Velero* station 1178, between lat 33°30′45″N, long 118° 30′40″W, and lat 33°27′40″N, long 118°30′00″W, 72 to 78 m, sand, 10 Sept. 1940. Identified by O. Hartman. AHF 003259, 1 specimen.

Off Upright Head, Lopez Island, Wash., approx. lat 48°35.5′N, long 122°53′W, 2 Aug. 1960. Collected by R. P. Dales and G. John. FHL 293, 1 specimen. New record.

South of Orcas Island, Wash., lat 48°34.9′N, long 122°50.8′W, 40 to 54 m, 13 Aug. 1964. Collected by S. van Niel. USNM 43636, 1 specimen. New record.

Additions to the Description: The two large complete animals from the San Juan Islands, Wash., were compared with the holotype. The slightly larger one (FHL) has about 65 abdominal setigers and is approximately 7.5 cm long (total) and 0.5 cm wide. The trunk of the Californian specimen (AHF) is slightly longer than 2.5 cm.

The branchial crown, previously unknown, contributes about one-fourth of the total length. The larger specimen has 30 pairs of radioles; in addition, about six pairs of nude filaments maximally one-fifth as long as the branchial crown are present. The palmate membrane connects three-fifths of the length of the radioles. Their free ends (Figure 5a) are 3 to 5 mm long and sometimes coiled up like a watch spring. The very numerous pinnules are about 1.5 mm long.

The collar (Figures 5b and 5c), well recognizable also in the holotype, is large for a species of *Chone*, markedly higher ventrally than dorsally and often opened and folded backward. When closed, it probably conceals fully the common basis of the radioles. The dorsal slit extends to the middle of the second setiger (Figure 5b). The first setiger is indistinctly set off from the first segment; the border is morphologically visible but is not indicated by a white line after staining (Figures 5c and 5d). The setae on the first setiger arise in a more ventral position than the notosetae on the following segments (Figure 5c).

Additions to Moore's description of the trunk are the following: A glandular postsetal girdle is present on the second setiger. The intrasegmental furrows in the middle and posterior thorax are not parallel to the intersegmental furrows (Figure 5e). Ventral shields are absent, i.e., the epidermis is completely glandularized and stains uniformly in the thorax and most of the abdomen, except for the inter- and intrasegmental furrows (Figure 5d).

Bayonet-type setae are present. The spatulate setae of the holotype, (stated by Moore, 1923, to be without a mucron) are lost and those of the Californian specimen are damaged. The spatulate setae of the material from Washington have hairs on their tips (Figure 5f). The thoracic uncini tend to be arranged in irregular double rows in the large animals. Anterior and posterior abdominal uncini (Figures 5g-i) have beaks longer than the bases, with three or four coarse accessory teeth above them. In frontal view, the teeth appear to be in a single row in most cases; occasionally I have seen two side by side. The difference in outline between Figures 5h and 5i is probably more a question of orientation than real.

Remarks: *Euchone magna* was transferred to *Chone* by Hartman (1969). It seems likely that Moore (1923) placed the species in *Euchone* due to a mistake while reconstructing his lost manuscript of 1911: His text states clearly the absence of a caudal membrane. Also, the vial contains a provisional label, *Chone magna*, which is written on stationery of the Philadelphia Academy and, according to Dr. M. H. Pettibone, is in Moore's handwriting.

The species has been known previously only from California.

CHONE ECAUDATA (MOORE)

Figure 6

JASMINIERA ECAUDATA Moore, 1923, p. 246.

CHONE ECAUDATA.- Hartman, 1942a, p. 135; 1969, p. 663.- Berkeley and Berkeley, 1950, p. 67; 1952, p. 124.

CHONE GRACILIS.- Berkeley and Berkeley, 1932, p. 315; 1942, p. 206; 1952, p. 123, in part.

CHONE MINUTA Hartman, 1944b, p. 280; 1969, p. 671.- Rioja, 1963, p. 218.

?*CHONE TERES*.- Okuda, 1934, p. 236; 1946, p. 171.- Imajima and Hartman, 1964, p. 365.

Diagnosis: A small *Chone* species with ventral shields. Six to eight radioles connected for approximately one-half of length by palmate membrane, with free ends of variable length. Collar low, almost level, barely covering the branchial basis, with overlapping dorsal ends. First bundle of setae large, on same level as following notosetae. Conspicuous rounded notopodial lips in thorax. Spatulate setae with long pointed tips. Anterior abdominal uncini with rostra longer than bases, with several rows of teeth in several columns; crowns posteriorly much higher, bases rounded.

Material studied: Two syntypes from off Santa Cruz, Calif. Dr. M. H. Pettibone (personal communication) suggested that following Moore's handwritten label, the smaller, complete specimen should be designated the holotype. USNM 17319.

Dillon Beach, Calif., July 1933. Collected by O. L. Williams; originally identified as *C. minuta*. AHF 003229, 11 specimens of a larger sample.

Fort Bragg, Calif., abundant in tunicate and *Lissodendoryx* colonies and eel grass, 29 June

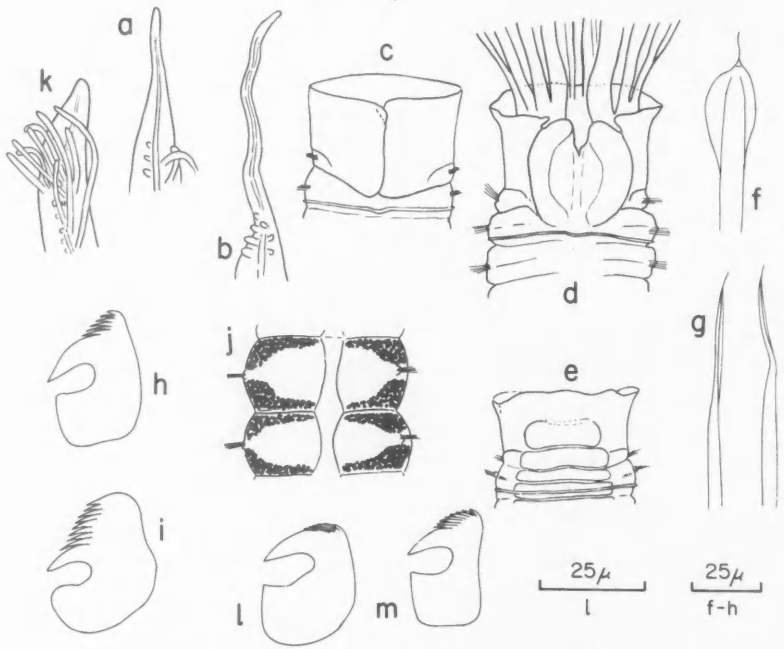

FIGURE 6.—*Chone ecaudata*; a-c, f from types d, e, and k from USNM 40304, h, i from AHF 2720, g, j from AHF 2721, l, m from USNM 45267: a, b, ends of dorso-lateral and ventralmost radioles; c, dorsal view of anterior end, branchial crown omitted (paratype); d, same view, with opened collar; e, ventral view of anterior end of specimen in Figure d; f, spatulate seta from third setiger; g, bayonet-type setae; h, i, largest and smallest uncini from 18th abdominal setiger (out of 25 total). Figure i is enlarged twice over Figure h; j, dorsal staining pattern in midthorax; k, end of lateral radiole; l, uncinus from third abdominal setiger; m, uncinus from 28th abdominal setiger, 20 μ high.

1934. Originally identified as *C. minuta*. AHF 003230, 5 specimens of a larger sample.

Holotype of *C. minuta* from Dillon Beach, Calif., in holdfasts of algae and among compound ascidians, 14 June 1941. AHF n 417; type AHF-67, Poly. 0182.

Wreck Bay, British Columbia, 1921 (see Berkeley and Berkeley, 1932, as *C. gracilis*). USNM 40722, 16 specimens.

Wreck Bay, west coast of Vancouver Island, 1925. Collected and identified by E. and C. Berkeley (see Berkeley and Berkeley, 1950). USNM 40303, 2 specimens.

Horsewell Point, British Columbia, in seaweed, 25 Apr. 1934. Collected by E. and C. Berkeley and identified as *C. gracilis*. USNM 40721, 2 specimens. Unpublished record.

Dodd's Narrows, British Columbia, 19 June 1957. Collected and identified by E. and C. Berkeley. USNM 40304, 1 specimen. Unpublished record.

Pavlov Bay, Alaska (see Berkeley and Berkeley, 1942, as *C. gracilis*). USNM 40723, 3 specimens.

Samami, Hokkaido, Japan, Aug. 1970. Collected by M. Imajima and identified as *C. teres*. USNM 45267, 3 specimens out of a much larger original sample.

Additions to the Description: The syntypes of *C. ecaudata* are mature females. The complete holotype has 18 abdominal setigers and is about 9 mm long (total); the paratype is a larger anterior fragment which is almost twice as wide.

A palmate membrane that "extends well over half the length of the radioles" (cf. Hartman, 1942a, p. 136) connects seven pairs of radioles bearing pinnules. A few pairs of nude filaments are present ventrally, the longest being almost half as long as the radioles proper. The ends of the radioles beyond the origin of the distal pinules are rather short dorsally (cf. Figure 6a). Laterally and ventrally, the ends can be "coiled like a watch spring" (cf. Moore, 1923, p. 246), having long filiform tips and being about a quarter as long as the entire radioles. A ventral radiole may be present, as long as the others but with an especially long terminal portion, the pinnules not extending as far as on the other radioles (Figure 6b; in one of the types, and USNM 40304).

The low collar barely conceals the bases of the branchial crown. When closed, it overlaps dorsally (Figure 6c); when open as in the holotype, it is formed as shown in Figure 6d (from another specimen; the outer heavy lines in this figure correspond to the edges of the collar in Figure 6c; the anterior incision extends almost to the level of the first bundle of setae in the holotype of *C. minuta*).

Ventral shields and intrasegmental furrows are more or less visible depending on the contraction of the animals (Figure 6e). After weak staining, however, the ventral shields and the biannulated character of the setigers are very distinct as far as the middle of the abdomen in all animals.

The first (buccal) segment (Figure 6e) is unusually large and distinct ventrally. The anterior border of the first setiger approaches the posterior border dorsad to the setae (Figures 6c and 6d). This bundle of setae is as large as those of the following notopodia and emerges on the same level. Rounded anterior and posterior notopodial lips are conspicuous. The limbate setae originate above the lips. All specimens have spatulate setae with long tips (Figure 6f). Bayonet-type setae, with shafts of the same diameter as the spatulate setae, are also present (Figure 6g). A thoracic uncinus of the holotype of *C. ecaudata* was figured by Hartman (1942a, Figure 15g). Other Californian material seems to have uncini with slight wings (Hartman, 1944b, Plate 23, Figure 51) as I have observed for a specimen from British Columbia (USNM 40304). Hartman (1942a, Figure 15f) depicted two abdominal uncini from anterior segments. No satisfactory view of posterior abdominal uncini was obtained from the type material. Anterior and posterior abdominal uncini differ in other California specimens. Anteriorly, four or five rows of accessory teeth in six to eight columns are situated above the rostrum; the rostrum extends beyond the basis (cf. Figure 6h; also Hartman, 1944b, Plate 23, Figure 50). Posteriorly, some uncini having the same shape occur in the same tori with smaller

ones that have higher crowns and more rounded bases (Figure 6i).

After staining of the types of *C. ecaudata*, the ventral shields in the thorax and abdomen are darkest, except for a small area on the anterior border of the first segment (cf. Figure 6e). Most parts of the collar, except for the anterior edge, are stained in the types but may be whitish in other specimens. Dark areas around the thoracic parapodia are separated from the shields by a spottily stained longitudinal band. This is especially obvious in specimens from British Columbia. In some of the other Californian animals (AHF 003230), the thorax seems to stain similarly laterally and ventrally under low power, but when viewed under 100 ×, the lateral areas appear in a granulated pattern, in contrast to the uniformly stained ventral region.

The dorsal pattern, beginning in the middle thoracic segments (Figure 6j), is present in all animals and seems to be very characteristic. It results from the widening of the nonstaining epidermis of the intrasegmental furrow. This pattern continues on the anterior abdominal setigers, but the unstained areas become progressively narrower until, in the middle part of the abdomen, the pale intrasegmental lines are as narrow as the intersegmental rings. In some Californian specimens (AHF, originally identified as *C. minuta*), a conspicuous subcircular spot of heavily stained cells straddles each intersegmental furrow at the level of the parapodia in the posterior thoracic and anterior abdominal segments. The staining pattern was not studied in the holotype of *C. minuta*.

The variability of the ends of the radioles is noteworthy; their shape is not related to size or the region where collected. In material from British Columbia (USNM 40303, 40304), a complete mature female, 11 mm long and 0.9 mm wide, has six pairs of radioles connected for two-thirds of their length by the palmate membrane. The free ends of the radioles scarcely extend beyond the ends of the pinnules (Figure 6k). Also within the samples from California, the length of the free ends of the lateral radioles is variable, sometimes being intermediate between that shown in Figures 6a and 6b, or is even shorter (cf. Hartman, 1944b, Plate 24, Figure 59). The Californian specimens (AHF), some of which are mature, are up to 15 mm long, and have up to 29 abdominal setigers and seven or eight pairs of radioles (usually connected for half of their length). Although in other species of *Chone* the width of the flanges (i.e., the extension of the palmate membrane) varies between the dorsal- and ventralmost radioles such that the ventral ones appear slimmer, the relative length of the free part is usually fairly consistent (see, however, *C. infundibuliformis*, p. 462).

Remarks: *Chone minuta* agrees with *C. ecaudata* by its size, the shape of the collar, the fairly distinct ventral shields, the form of the spatulate setae and anterior abdominal uncini, and the dorsal staining pattern in the thorax (the last character was not checked in the holotype of *C. minuta*). The variability in the length of the free ends of the radioles of the specimens originally described as *C. minuta* is notable.

Among the material identified by the Berkeleys as *C. gracilis*, the lot from Horsewell Point (USNM 40721) allowed staining; the pattern, in addition to the form of the branchial crown, the collar, the ventral shields, and the form of the spatulate setae make identification certain. The lot from Wreck Bay (USNM 40722) is referred here with some hesitation because of the bad preservation. The branchial crown, ventral shields, and the form of spatulate setae, however, agree with *C. ecaudata*. Berkeley and Berkeley had recorded *C. ecaudata* from Wreck Bay in 1950.

With considerable hesitation, Japanese material from Hokkaido, originally identified by Dr. M. Imajima as *C. teres*, is included here. These specimens correspond closely to the description of *C. teres* by Okuda (1934), which, however, does not refer to *C. infundibuliformis* (cf. p. 461). The collars are of even height ventrally and laterally but are lowered dorsally, which is not the case in typical *C. ecaudata* (cf. Okuda, 1934, Figure 3). The radioles end as shown in Figures 6a and 6k. The uncini from anterior segments differ considerably from those in posterior segments (Figures 6l and 6m). The staining pattern dorsally in the thorax is similar to that of *C. ecaudata* (Figure 6j) except that the

pigment-free areas in the middle of the segments are narrower. The main difference between the specimens from Hokkaido and typical *C. ecaudata* is the apparent absence of ventral shields, both morphologically and in fully stained specimens; the distribution of stain-absorbing cells seems to be uniform ventrally of the setae. In animals where the dye has almost been differentiated, however, one does see stronger staining ventrally, and the indication of a whitish line ventral to the parapodia. The Japanese animals are included in *C. ecaudata*, in spite of the fact that the ventral shields seem to be almost absent, because of the general agreement with the typical form and because of the transitional character of specimens from Alaska (USNM 40723). Here, the collar is formed as in Japanese material, but morphologically distinct shields are present. Staining was not possible. Evidently, additional collections are needed for the study of the Alaskan and northwest Pacific forms. The record of *C. teres* by Uchida (1968) cannot be identified from the brief description.

CHONE ENIWETOKENSIS (REISH) NEW COMBINATION

EUCHONE ENIWETOKENSIS Reish, 1968, p. 225.

Material studied: Holotype (USNM 38406) and paratype (USNM 38407), from the Marshall Islands.

Diagnosis: A very small *Chone* species with weakly developed ventral shields and 13 to 14 abdominal setigers. Three to four pairs of radioles connected by palmate membrane for one-third of length. Collar oblique. Subspatulate setae with very long pointed tips. Abdominal uncini uniform, with a few teeth; rostra larger than bases.

Additions to the Description: The collar is higher ventrally than dorsally and has a broad, midventral lowering of the anterior edge. The postsetal girdle of glands is present on the second thoracic setiger. The holotype, but not the paratype, has a similar but somewhat irregular ring also on the fifth setiger. The fifth setiger of the paratype does not appear to be damaged, although otherwise the paratype is somewhat macerated. The ventrum of the thorax stains strongly; however, ventral shields could not be distinguished morphologically. The posterior end is strongly compressed dorso-ventrally suggesting, in unstained material, an anal depression. Treatment with methyl green showed uninterrupted segmental rings of staining cells around the posterior ends.

Remarks: This species is referred to *Chone* because the posterior end lacks the anal depression typical of *Euchone*. The species is not yet well characterized; moreover, it is not known whether the specimens were fully grown. If the fifth thoracic setiger indeed carries a glandular ring, the species would be uniquely distinguished.

CHONE VELERONIS NEW SPECIES

Figure 7

Holotype: From *Velero* station 6104, lat 33°39′45″N, long 118°06′40″W, 26 m, dark gray silty fine sand, 19 Feb. 1959. AHF Poly. 0459.

Paratypes: Same station and date. AHF Poly. 0460 (>10 specimens).

Diagnosis: A small species of *Chone* without ventral shields, with a greatly broadened postsetal girdle of glands on second setiger. Branchial crown long, with very high basis and six to seven pairs of radioles with filiform free ends. Collar low. Palmate membrane reaching beyond distal pinnules. Spatulate setae with pointed tips. Anterior abdominal uncini markedly different within tori, largest with small teeth, rostra as long as bases; small uncini with greatly enlarged crown. Posterior uncini only of the latter kind.

The species is named after the present ship of the Allan Hancock Foundation, the *Velero IV*, which collected the specimens.

Material studied: About 10 specimens of the type series.

Description: Mature animals, with about 45 abdominal setigers, are 11 to 12 mm long, of which approximately 3 mm are contributed by the branchial crown, and 0.5 to 0.6 mm wide. The smallest animal at hand has about 35 abdominal setigers and is 5 mm long and 0.3 mm wide. All specimens are well preserved.

The branchial crown has six to seven pairs of radioles, on an unusually high basis (Figure 7a). The radioles are connected by a palmate membrane that extends beyond the origin of the distal pinnules (Figure 7b). The narrow free tips are one-eighth to one-sixth as long as the radioles. Nude filaments were not found.

The low collar usually does not conceal the anterior part of the first (buccal) segment fully; it is somewhat higher ventrally than laterally (Figure 7a and 7c) and entire, except for the dorsal slit which reaches to the intrasegmental furrow of the second setiger. The first segment is sometimes distinct ventrally (Figure 7a). The posterior border of the first setiger does not quite extend to the fecal groove. Segments, except the first one, are biannulate in the thorax and the anterior half of the abdomen. The thoracic intrasegmental furrows bend rearward similar to those of *C. magna* (cf. Figure 5e). The postsetal glandular girdle of the second setiger (Figure 7a) is ventrally greatly broadened, extending into the third setiger. Laterally it is narrowed but still broader than on the dorsal side where it is similar in width to that of other species of *Chone*. The girdle has the same shape in the smallest animal available. A longitudinal band of whitish glandular tissue extends midventrally from the girdle onto the collar. Similar tissue is present is rings near the anterior edges of the posterior thoracic and about half of the

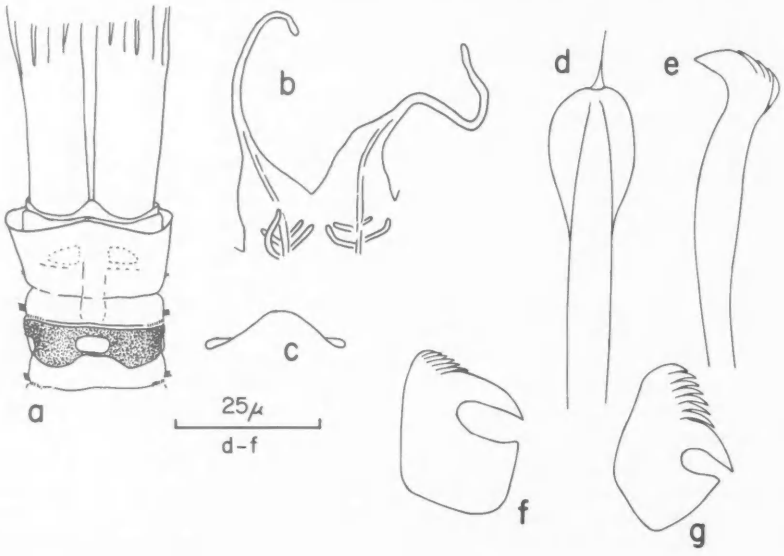

FIGURE 7.—*Chone veleronis* new species; a and c from holotype, rest from paratypes; d, f, not drawn to scale: a, ventral view of anterior end. Horizontal broken line in collar indicates anterior border of first setiger seen occasionally. The two areas on the collar encircled by broken lines remain whitish after staining with methyl green. The glandular girdle has been dotted; b, tips of two radioles; c, collar of another specimen in same view as in a; d, spatulate seta; e, thoracic uncinus; f, large uncinus from anterior abdominal setiger; g, uncinus from 40th abdominal setiger from median position in torus, 17 μ high.

abdominal setigers. The pygidium is triangular and pointed. Eggs occur from the sixth thoracic setiger.

The inconspicuous first bundle of setae originates at the level of the following notopodia. These have four to six of each upper limbate, very tiny bayonet, and pointed spatulate (Figure 7d) setae. Notopodial lips were not seen. Thoracic neuropodia contain slightly more than half a dozen long-handled uncini (Figure 7e). Abdominal setigers carry approximately half a dozen finely limbate neurosetae and, at least through the 40th setiger, 12 to 15 uncini. The uncini from the anterior abdomen, in the most recently formed sections of the tori, are of the usual form of *Chone* (Figure 7f) with several columns of five to six accessory teeth each. The smallest, i.e., oldest, uncini of these tori, and all uncini in posterior segments (Figure 7g), have smaller bases and appear similar to the uncini of *Oriopsis*. The posterior uncini have about six columns of about seven teeth each.

Staining with methyl green shows the absence of ventral shields. The whole surface in the anterior half of the body accepts the dye uniformly except for the anterior edge and ventral parts of the collar (cf. Figure 7a), the inter- and intrasegmental furrows, and the glandular girdle on the second setiger. Ventrally, the anterior border of the first setiger, which is often invisible in unstained material, is marked as a whitish line. The presetal rings of glandular tissue stain less well than the rest of the epidermis. On the posterior half of the abdomen only few epidermal cells accept the stain.

Remarks: Hartman (1959, 1965) has listed the species of *Chone*, to which *C. rosea* Hartmann-Schröder, *C. striata* Hartmann-Schröder, *C. trilobata* Gallardo, and *C. albocincta* described below should be added. Among these, *C. veleronis* is distinguished by the ventral enlargement of the postsetal glandular girdle on the second setiger, the very long branchial bases, and the length of the palmate membrane. Only very few species (e.g., *C. arenicola* Langerhans) have a palmate membrane extending beyond the origin of the distal pinnules.

CHONE ALBOCINCTA NEW SPECIES

Figure 8

Holotype: From *Velero* station 6104, lat 33°39′45″N, long 118°06′40″W, 26 m, dark gray silty fine sand, 19 Feb. 1959. AHF Poly. 0454.

Paratypes: From same station and date. AHF Poly. 0455, three adults or near-adults, nine juveniles.

Diagnosis: A *Chone* species of intermediate size without ventral shields. Branchial basis slightly longer than the slightly oblique collar. Eight to ten pairs of radioles, connected by palmate membrane up to origins of distal pinnules, with abruptly tapered filiform free ends. Presetal whitish rings of tissue in thorax; presetal and postsetal whitish rings in anterior and median abdomen. First bundle of setae small, on same level as following notosetae. Spatulate setae with pointed tips. Anterior abdominal uncini markedly different within tori, smallest with rounded bases and high crowns. Posterior abdominal uncini predominantly of latter type.

The name of the species refers to the whitish rings contrasting in unstained animals with the red-brown color of the remaining epidermis.

Material studied: Type series.

Description: The holotype is a mature female with 8 thoracic and approximately 50 abdominal setigers. The total length is about 18 mm, the greatest width is 1 mm. The branchial crown measures about 6 mm. Two other adult animals of 51 and 52 abdominal setigers are slightly larger (total 20 mm; branchial crown, 7 mm) and somewhat shorter than the holotype. The juveniles have trunks about 5 mm long and the same body proportions. All specimens are well preserved.

The branchial crown has a base slightly longer than the collar and 9 to 10 pairs of radioles which are united by the palmate membrane up to the insertion of the distal pinnules. A 0.2-mm broad flange extends for a short distance beyond this point but tapers abruptly to a filiform free end (Figure 8a). The free ends of the radioles are

from one-fifth to one-sixth the length of the total radioles. The ends of the radioles surpass the ends of the distal pinnules. Ventral nude filaments were not seen.

The collar (Figures 8b and 8c) is oblique, with entire margin. The first (buccal) segment is invisible and the collar is not clearly set off from the first setiger; the border can be recognized only in stained material. The thoracic and 15 to 20 anterior abdominal setigers are clearly biannulate; after staining also the following ones appear divided. Ventral shields are absent. A thick glandular postsetal girdle is present on the second setiger. Dorsally in the thorax, the intrasegmental borders bend rearward similar to *C. magna* (cf. Figure 5e). Rings of elevated whitish tissue, presumably glandular, are present in the presetal annuli of the thoracic setigers and in the presetal and postsetal annuli of the anterior 15 to 20 abdominal setigers. The ring on the second thoracic setiger is ventrally expanded (Figure 8b). Except on the second se-

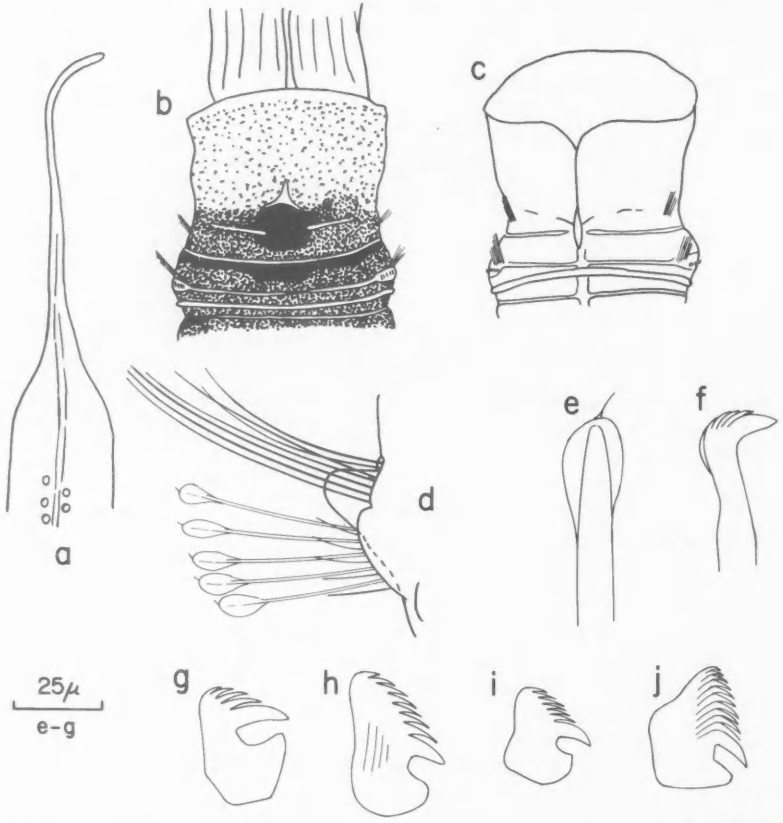

FIGURE 8.—*Chone albocincta* new species, from large types; abdominal uncini not to scale: a, end of median radiole; b, ventral view of anterior end, showing staining pattern; c, dorsal view of anterior end, branchial crown omitted; d, anterior view of fourth notopodium; e, spatulate seta; f, thoracic uncinus; g, large uncinus from fourth abdominal setiger (about 30 μ high); h, small uncinus from ninth abdominal setiger; i, j, small and large uncini from approximately 40th abdominal setiger.

tiger, the rings are invisible after using methyl green, which stains the setigers in question uniformly except for the inter- and intrasegmental furrows. Posterior to the 15th to 20th abdominal setiger, the stain is accepted by numerous, distinct cells arranged in presetal and postsetal bands. These bands coalesce in the posterior part of the abdomen.

The first bundle of setae, slightly smaller than the following ones, inserts in the collar at the same level as the following notopodia (Figure 8c). The notopodia have small lips (Figure 8d) and long limbate, bayonet-type and narrow spatulate setae; the latter have pointed tips (Figure 8e). The thoracic uncini, with small wings (Figure 8f) are arranged in single rows.

Anterior abdominal parapodia have about 30 uncini. The large (ontogenetically most recent) uncini (Figure 8g) have squarish bases and three to four rows of four or five coarse teeth. The uncini change gradually within the torus into smaller hooks (Figure 8h) with rounded bases and somewhat more teeth (five on the fourth setiger, seven on the ninth). In the posterior abdomen, the smallest uncini of a torus are similar (Figure 8i; about 10 columns of teeth); the largest ones (Figure 8j), however, have very broad posterior portions and crowns with more numerous teeth in approximately half as many rows.

Juveniles of about 5-mm trunk length and 0.4- to 0.5-mm width, with about 35 abdominal setigers, show the white rings clearly. Staining with methyl green, however, indicates that the glandularization of the epidermis is not complete. The dye-absorbing cells are distributed principally along the edges of the stained areas so that the centers of the areas are light.

Remarks: *Chone albocincta* seems to be distinguished from all other species of the genus (cf. p. 479) by the whitish segmental rings of tissue. Somewhat similar presetal rings, however, also occur in *C. veleronis* described above. Neglecting differences in size, *C. albocincta* may be separated from the northeast Pacific species without ventral shields (*C. aurantiaca, C. duneri, C. infundibuliformis, C. magna, C. mollis,* and *C. veleronis*) also by the following: the postsetal glandular girdle on the second segment is narrow ventrally (from *C. veleronis*); the first segment is indistinguishable in the first segment in unstained animals (from *C. mollis*); the radioles have long free ends (from *C. aurantiaca* and *C. infundibuliformis*); the abdominal uncini have coarse teeth (from *C. duneri*). *Chone magna* has spatulate setae without pointed tips and only one form of abdominal uncini.

EUCHONE MALMGREN, 1866 EMENDED

EUCHONE Malmgren, 1866, p. 405.- Langerhans, 1881, p. 111.- Saint-Joseph, 1894, p. 250.- Bush, 1904, p. 190.- Hofsommer, 1913, p. 327.- McIntosh, 1923, p. 281.- Fauvel, 1927, p. 339.- Berkeley and Berkeley, 1952, p. 121.- Ushakov, 1955, p. 418.- Day, 1967, p. 774.- Banse, 1970, p. 389.

Type species: *Euchone analis* (Kröyer) (cf. Bush, 1904).

Diagnosis: Sabellidae with semicircular branchial lobes sometimes united by palmate membrane. Collar conspicuous, sometimes bilobed. Postsetal girdle of glands on second setiger. Ventral shields sometimes present. Anal depression with lateral wings formed by variable number of caudal segments. Three types of thoracic notosetae: upper, or upper-anterior ones limbate; lower, anterior ones narrowly limbate (bayonet-type); and lower, posterior ones spatulate or usually subspatulate. Thoracic neuropodial uncini long-handled, acicular. Abdominal notopodial uncini avicular, with rounded or square bases; abdominal neurosetae limbate.

Remarks: The genus continues to comprise all Fabriciinae with an anal depression. Added to previous diagnoses are presence or absence of the palmate membrane, the note about the collar, the postsetal girdle of glands, the bayonet-type setae, and the ventral shields. The last three characters had previously been mentioned by Banse (1970). It must be noted that *E. alicaudata* Moore, known so far only from one specimen, possibly lacks bayonet-type setae (cf. p. 489). The number of thoracic setigers (almost

always eight) is not considered as a diagnostic character for this genus.

Of great consequence for the systematics of the Sabellidae is the opinion that the number of lobes in the collar and the presence or absence of a palmate membrane are specific characters in *Euchone*. Therefore, they cannot be used for dividing genera (cf. p. 459 and 461). The reason is my opinion that the anal depression is of monophyletic origin and therefore a primary character, sufficient to characterize *Euchone*.

EUCHONE ANALIS (KRÖYER)

Figure 9a-c

SABELLA ANALIS Kröyer, 1856, p. 17.
EUCHONE ANALIS.- Malmgren, 1866, p. 406; 1867, p. 223.- Berkeley and Berkeley, 1952, p. 121.- Pettibone, 1954, p. 339 (synonymy).- Hartmann-Schröder, 1971, p. 521.
not *EUCHONE ANALIS* Imajima, 1963, p. 367.

Diagnosis: A *Euchone* species with ventral shields, with 16 to 22 anterior abdominal setigers and 9 to 12 setigers in anal depression. Nine to 17 pairs of radioles united by palmate membrane for half their length, with free ends tapered, intermediate in length; 5 to 10 pairs of ventral nude filaments. Collar level, with slight ventral incision, almost concealing the branchial basis. Lower thoracic notosetae subspatulate. Uncini from anterior and posterior abdomen similar, with squarish bases.

Material studied: Point Barrow, northern Alaska, about 65 m. Identified by M. H. Pettibone (cf. Pettibone, 1954). USNM 23651, 1 specimen.

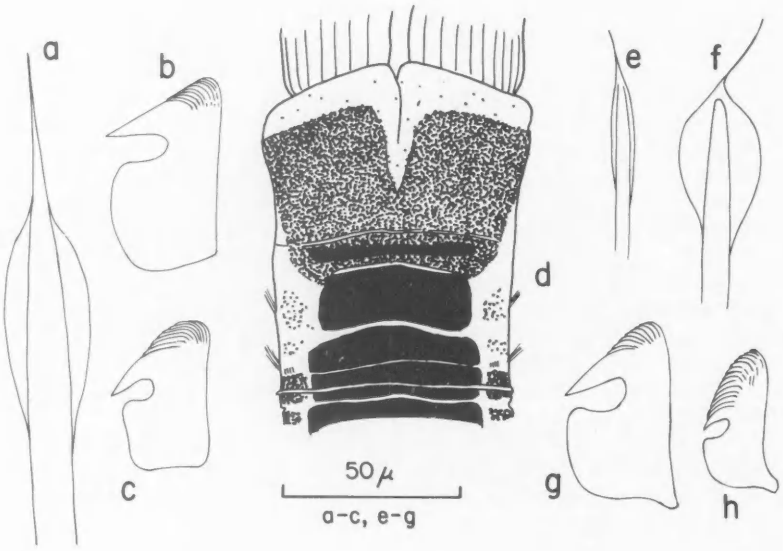

FIGURE 9.—*Euchone analis*: a, subspatulate notoseta; b, median uncinus from third abdominal setiger; c, same, from 21st. Accessory teeth schematic; *E. papillosa*: d, anterior end of thorax, ventral view, showing staining pattern; e, bayonet-type seta; f, spatulate seta; g, median uncinus from third abdominal segment; h, uncinus from anterior depression segment, approximately one and a half times enlarged over Figure g.

Addition to the Description: The specimen is complete. The length of the trunk is about 15 mm, that of the branchial crown approximately 4 mm. The branchial crown consists of some ventral nude filaments (5 to 10 pairs according to Kröyer, 1856, and Malmgren, 1866), and 10 pairs of radioles bearing pinnules and connected by a palmate membrane. The ends of the radioles are like those of *E. elegans* (cf. Figure 11a). The collar has a small ventral incision. The second setiger is ringed by a postsetal girdle of glands. Segments are biannulate up to the anal depression. There are 17 anterior abdominal segments and 9 setigers in the anal depression. Ventral shields are present in thorax and abdomen. The shields of the first segment and first setiger are divided by intrasegmental furrows which do not stand out as whitish lines after staining. In the abdomen the shields have the form depicted by Malmgren (1866, Plate 28, Figure 88).

The notopodia, including the large first one, have conspicuous lips of the same form as *E. rubrocincta* (cf. Figure 10d). The bayonet-type setae have shafts almost as thick as the subspatulate ones (Figure 9a) behind them and are terminally thin, as usual. Anterior abdominal uncini (Figure 9b) are all alike within the tori; each has a squarish basis and a crown of about 10 rows of accessory teeth in several columns. The bases of the posterior uncini (Figure 9c) are similar but the crowns have about 15 rows of teeth in approximately a dozen columns.

After staining, the ventral shields and, separate from them, areas before and behind the parapodia are conspicuous in thorax and abdomen. The first setiger does not seem to be separated from the preceding and following segments by nonstaining lines, nor is the intrasegmental furrow distinct. The intrasegmental furrow on the second setiger resembles that of *E. rubrocincta* (Figure 10c). Dorsally, the thorax and the anterior segments of the abdomen are essentially free of stain-accepting cells. In middle and posterior abdominal setigers, presetal broad rings are complete; they are visible as whitish tissue also in the unstained animal.

Remarks: This specimen has 17 anterior abdominal setigers, fewer than stated by Malmgren (1866, about 19) and Berkeley and Berkeley (1952, 20 to 22) but similar to Kröyer (1856, about 16). More material must be studied in order to see whether the number of anterior abdominal setigers overlaps those of the similar *E. elegans* and *E. rubrocincta*. If so, a probably reliable difference of *E. analis* from the others will be the form of the anterior abdominal uncini.

The record by Imajima (1963) from the west coast of Kamchatka is not this species because of the low number of anterior abdominal setigers and the high number of segments in the anal depression.

EUCHONE PAPILLOSA (SARS)

Figure 9d-h

SABELLA PAPILLOSA Sars, 1851, p. 203.

EUCHONE PAPILLOSA.- Malmgren 1866, p. 407.- Hofsommer, 1913, p. 327.- Augener, 1928, p. 805 (synonymy).- Evenkamp, 1931, p. 412.- Pettibone, 1956, p. 578 (synonymy).- Kühlmorgen-Hille, 1963, p. 51.- Hartmann-Schröder, 1971, p. 521.

SABELLA TUBERCULOSA Kröyer, 1856, p. 18.

EUCHONE TUBERCULOSA.- Malmgren, 1866, p. 407.

Diagnosis: A large *Euchone* species with ventral shields, with at least 21 abdominal setigers; 8 to 10 form anal depression. Ten to 15 pairs of radioles connected for approximately one-half their length by palmate membrane, with long filiform free ends. Two to five pairs of ventral nude filaments. Collar oblique, with midventral incision, scarcely concealing the branchial basis. Very conspicuous round fields of glands ventrally in abdomen. Spatulate setae with very long tips. Uncini of anterior abdomen with small crowns of teeth and bases with posterior extension; markedly higher crowns in posterior abdomen.

Material studied: Kiel Bight, western Baltic (unknown locality). Collected and identified by G. Kühlmorgen-Hille (cf. Kühlmorgen-Hille, 1963). Part of sample, USNM 45390, 6 specimens.

Additions to description: Because the species is well known, only some characters have been studied, mostly for a comparison with *E. capensis* Day and *E. velifera* new species, both of which also have collars with ventral incisions. The animals studied were fixed in their tubes, are up to 2.5 cm long, and are well preserved.

The radioles have free filiform ends as shown by Malmgren (1866, Plate 29, Figure 92G but not 94G). The collar (Figure 9d) is markedly longer ventrally than dorsally. The number of abdominal segments in six animals is 21, 21, 22, 23, 23, and 24, of which 8 to 10 form the anal depression. Similarly Hofsommer (1913) found specimens from the western Baltic, which he believed to be juveniles, with a total of 29 segments (= setigers, from the context) and stated that in adults the number is constantly 35, similar to Malmgren (1866). Evenkamp (1931) in material from Kiel Fjord, however, observed up to 62 segments of which, again, 8 were thoracic.

Thoracic notopodia contain broad bayonet-type setae (Figure 9e) and spatulate setae (Figure 9f). The spatulate setae in the present material are broader than those depicted by Malmgren (1866, Plat 29, Figures 92B[1] and 94B[1]). The uncini on anterior abdominal segments (Figure 9g) have broad bases with small posterior appendages and crowns with approximately 10 columns with 10 to 13 teeth each, depending on the size of the uncini. Posteriorly in the abdomen, the bases of the uncini become more rounded, and there are about 15 rows of teeth in much enlarged crowns (Figure 9h).

The thoracic and abdominal ventral shields are very conspicuous even in unstained material (cf. Malmgren, 1866, Plate 29, Figures 92 and 94). After using methyl green, the ventral pattern in the anterior thorax is as shown in Figure 9d. Laterally in the thorax, crescentic areas of stained tissue occur posterior to the parapodia and to a lesser degree anterior to them. The dorsal side of the thorax is unstained except for a pair of conspicuous rounded areas near the anterior border of each segment from the 4th setiger onwards. In the anterior and middle regions of the abdomen, each setiger shows ventrally two pairs of rounded patches, one near the anterior and one near the posterior border. These have been figured first by Malmgren (1866, Plate 29, Figures 92 and 94). Their size varies among individuals; they sometimes occupy almost half of the ventral area of the segments. Laterally in the abdomen, the stained tissue around the parapodia, observed in the thorax, becomes gradually larger and extends onto the dorsal side so that from the middle of the abdomen, a pigmented band crosses the posterior part of the segments (the parapodia insert here posteriorly on the segments). In the same region, the anterior dorsal patches coalesce. Shortly before the depression segments, the intrasegmental furrows disappear and each segment is uniformly stained both dorsally and ventrally.

EUCHONE RUBROCINCTA (SARS)

Figure 10

CHONE RUBROCINCTA Sars, 1862, p. 128.
EUCHONE RUBROCINCTA.- Malmgren, 1866, p. 406.- Southern, 1914, p. 144.- McIntosh, 1916, p. 33; 1923, p. 282.- Southward, 1956, p. 278.

Diagnosis: A *Euchone* species with conspicuous ventral shields, with 11 to 15 anterior abdominal setigers and up to 12 setigers in anal depression. Up to 16 pairs of radioles united by palmate membrane for about half their length, with long free ends. Up to eight pairs of nude filaments. Collar level, with a small ventral notch. Lower thoracic notosetae subspatulate. Uncini of anterior abdomen with small crowns of teeth, slim necks, and narrow bases with marked posterior extensions. Uncini of posterior abdomen with large crowns, without necks.

Material studied: Syntypes, from Florø, near Bergen, Norway, approximately lat 61°40′N, long 5°00′E, stony bottom (Sars, 1862). ZMO, 3 specimens.

Ballynakill Harbour, Northwest Ireland, stations L 245, L 310, and ML L 11a (cf. Southern,

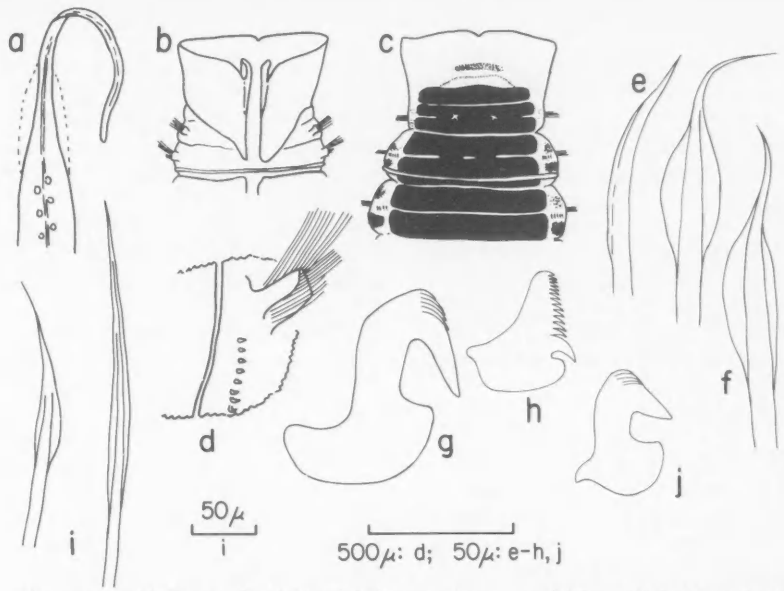

FIGURE 10.—*Euchone rubrocincta*; b-h from syntypes, a and i from NMI, j from Southward's material: a, end of representative radiole. Broken line indicates extent of flange in syntypes (see also text); b, dorsal view of anterior end, branchial crown omitted; c, ventral view of anterior end, branchial crown omitted, after staining. Slightly schematic; x indicates the extent of the incision of the ventral shield on the first setiger of *E. elegans*; d, part of lateral body wall of second setiger, seen slightly from below and behind, with setae and glandular girdle; e, f, bayonet-type and two subspatulate setae from fifth thoracic setiger; g, anterior abdominal uncini (seventh abdominal setiger). Accessory teeth schematic; h, uncinus from depression segment (17th abdominal setiger); i, subspatulate and limbate setae from sixth thoracic setiger; j, uncinus from seventh abdominal setiger.

1914). NMI 77.1908, 1 specimen from each station.

Irish Sea, station 22 of Southward (1956, 1957). Dr. E. C. Southward's private collection. 3 specimens.

Additions to the Description: The largest of the well-preserved syntypes, a fairly relaxed specimen, is approximately 2.5 cm long of which about one-fourth is contributed by the branchial crown. The width is about 2 mm. The other syntypes are approximately two-thirds as long; in one of them, a mature female, the branchial crown contributes about one-third of the total length, in the other one it is lost.

The branchial crowns of the two complete specimens consist of 10 and 13 pairs of radioles with pinnules and up to 8 pairs of slender naked ventral filaments. Two to three pairs of the latter are very short, and one or two pairs are as long as the radioles. The radioles are united for about half their length by a conspicuous palmate membrane. They end in bare tips, proximally broad owing to the continuation of the palmate membrane, but narrow in the terminal sections. The latter tend to be shorter ventrally than dorsally and are, on the average, about half as long in the syntypes as in the material from northwestern Ireland (Figure 10a). The length of the sections of the radioles free of pinnules is very approximately one-eighth of

the total length in the syntypes and in Southern's material.

In the syntypes, the collar is of equal height dorsally and ventrally and has only a small ventral notch (Figures 10b and c). Setigers are biannulate, which is especially obvious in the thorax. In the three syntypes, there are 11 anterior abdominal, 1 transitional, and 11 depression setigers; 15, 1, 9; and 12, 0, 10 setigers, respectively. Ventral shields are distinct in the thorax and abdomen as depicted by Malmgren (1866, Plate 29, Figure 91).

The thoracic notopodia (Figure 10d) are very conspicuous; each contains about a dozen each of long limbate, short bayonet-type (Figure 10e), and subspatulate (Figure 10f) setae. The long limbate setae originate above the semicircular lip shown in Figure 10d which is about 0.2 mm long; the other two kinds below it. Each neuropodium contains approximately 1½ doz of long-handled hooks of the usual form (cf. McIntosh, 1923, Plate 131, Figure 2a). The uncini of the anterior abdomen (Figure 10g; cf. Figure 10j) do not have the squarish basis usually found in *Euchone* species but have a slim neck and a large posterior extension making them almost S-shaped. Even the dorsalmost ones in the tori studied have essentially this outline. Only a few columns of teeth are found in these uncini. The uncini of the depression segments are formed as shown in Figure 10h; they have approximately eight columns of teeth, and the number of rows is 12 to 14. The number of uncini is about 2 doz per torus anteriorly in the abdomen and in median segments of the anal depression. The abdominal capillary setae are arranged in two series per neuropodium.

After using methyl green, the collar (Figure 10c) is lightly stained except for a ventral unstained area and, in some animals, a diffuse band anterior to it. The thoracic ventral shields are clearly marked. Laterally strongly staining areas are found posterior to and, to a lesser degree, anterior to the thoracic parapodia. In the last thoracic segments, these areas touch the ventral shields but do not continue onto the dorsal side, except as traces. In the abdomen, however, the stained cells form two girdles around each segment, interrupted only by the fecal groove; the presetal ring, which may appear dorsally as whitish glandular tissue even in unstained material, stains more strongly than the postsetal one. The ventral shields are not markedly darker after staining than the lateral and dorsal parts. The intersegmental unstained furrows disappear gradually in the depression segments.

In the material from northwestern Ireland, the largest animal, a mature male, is almost 2.5 cm long, of which about one-third is contributed by the branchial crown; the smallest specimen is 1.5 cm long. The latter has 11, the former, 15 pairs of radioles, with about 4 doz pairs of pinnules each. In all specimens, there are 12 anterior abdominal setigers, the twelfth sometimes appearing to be a transitional segment, and 10 to 12 depression segments. The notopodia (cf. Figure 10d) appear to be divided into anterior and posterior lips, rather than form one semicircular fold. Limbate and subspatulate notosetae are shown in Figure 10i; the total number of notopodial setae is 2 doz. The other characters agree with the syntypes.

No color is left in the syntypes of the Irish material, but Southern (1914) stated that the bright red bands, which gave the species its name, were present in Formalin-preserved material until the transfer into alcohol. Sars (1862) observed one purple ring on each segment.

McIntosh (1916) reported on animals with 15 to 16 pairs of radioles. It must be noted that McIntosh's description (1916, also 1923) of other features of the branchial crown contains quotations of Southern's (1914) text for *E. rosea*.

Southward's specimens are small, up to 7 mm long. Two have 11 anterior abdominal setigers, and one transitional setiger; the third animal has 13 or 14 anterior abdominal setigers. An uncinus from this region (Figure 10j) has a broader neck than the material treated above but otherwise has the same characteristic form. The staining pattern is as described by the syntypes as far as this can be recognized in the previously dried specimens.

Remarks: *Euchone rubrocincta* is close to the smaller *E. elegans* Verrill from which it is

distinguished by the larger number of radioles with long slender ends, and especially the form of the anterior abdominal uncini. Further, the incision of the ventral shield at the level of the first parapodium is very short in *E. rubrocincta* (see also *E. analis*, p. 483). *E. rosea* Langerhans, as described by Banse (1970) for specimens from the Ivory Coast, is very similar in regard to the tips of the radioles, the collar, the subspatulate notosetae, and especially the abdominal uncini. However, the ventral shield on the first setiger is not divided, and the number of anterior abdominal setigers is only 10 or 11, and that of the anal depression only 6. The smaller number of radioles in the African material may be due to their smaller size.

The distribution of the species is not well known. Material of Southern (1914) and Southward (1956) collected around Ireland has been treated above. The specimens of Malmgren (1866) from the Skagerak and McIntosh (1916, 1923) from the Shetlands are certainly *E. rubrocincta*. The species is also reported from the Mediterranean Sea (cf. Fauvel, 1927), but I have not searched the literature for Lusitanian and more southern records. Also, the reports of *E. rubrocincta* from the northwest Atlantic by Moore (1909) and Baillie (1946) should be checked because of the possible confusion with *E. elegans* treated below. The former author did not give any reference for identification; the latter referred to Malmgren's description.

EUCHONE ELEGANS VERRILL

Figure 11a-e

EUCHONE ELEGANS Verrill, 1873, p. 618.-Hartman, 1944a, p. 334 (with other references).

Diagnosis: A *Euchone* species with ventral shields, with 12 to 15 anterior abdominal setigers and 8 to 10 setigers in anal depression. Six to eight pairs of radioles, united by palmate membrane for about half their length, and rather broad and free ends. Three to four pairs of nude filaments. Collar level, with small ventral notch. Lower thoracic notosetae subspatulate. Marked divergence of uncini within tori of anterior abdomen; ontogenetically recent uncini with broad bases and small posterior extension; old uncini with rounded bases and high crowns, similar to those in depression.

Material studied: Syntypes, collected from Block Island Sound, Mass., in 1871. USNM 7513, 5 specimens.

Cape Cod Bay, Mass., SEP station 1412 E5, lat 41°55.0′N, long 70°08.5′W, 33 m, muddy sand, 11 June 1968. SEP, 4 specimens. Unpublished record.

Cape Cod Bay, Mass., SEP station 2318 Ep, lat 41°45.0′N, long 70°06.5′W, 16 m, sand, 13 Oct. 1966. SEP, 22 specimens. Unpublished record.

Additions to the Description: The available specimens are up to 1 cm long; about one-third of the length is contributed by the branchial crown. Verrill (1873) observed animals up to 2 cm long. Most of the branchial crowns have seven pairs of radioles with up to 3 doz pinnules each and three to four pairs of ventral nude filaments; one pair of these is about as long as the radioles. The free ends (Figure 11a) contribute about one-sixth of the total length of the radioles. The collar is of equal height dorsally and ventrally and has only a small ventral notch. Segments are biannulate, particularly in the thorax. A postsetal girdle of glands is present on the second setiger. Ventral shields are moderately visible in unstained material in the thorax and anterior abdomen but stand out clearly upon staining. In the syntypes, the number of abdominal setigers is 13 (12 in one) followed by 1 transitional and 8 depression setigers. In the 10 SEP specimens, up to 9 mm long, 15 setigers are present prior to the beginning of the depression in 7 specimens; 14 setigers in 2 specimens; and 14 or 15 in 1 specimen. The anal depression extends through 10 setigers in the largest animals.

The thoracic notopodia are almost as conspicuous as in *E. rubrocincta* (cf. Figure 10d). Each contains long limbate, short bayonet-type, and subspatulate (Figure 11b) setae, totaling less than a dozen. Each neuropodium has about 10 long-handled hooks. The uncini of the anterior abdominal segments (Figure 11c) have a broad

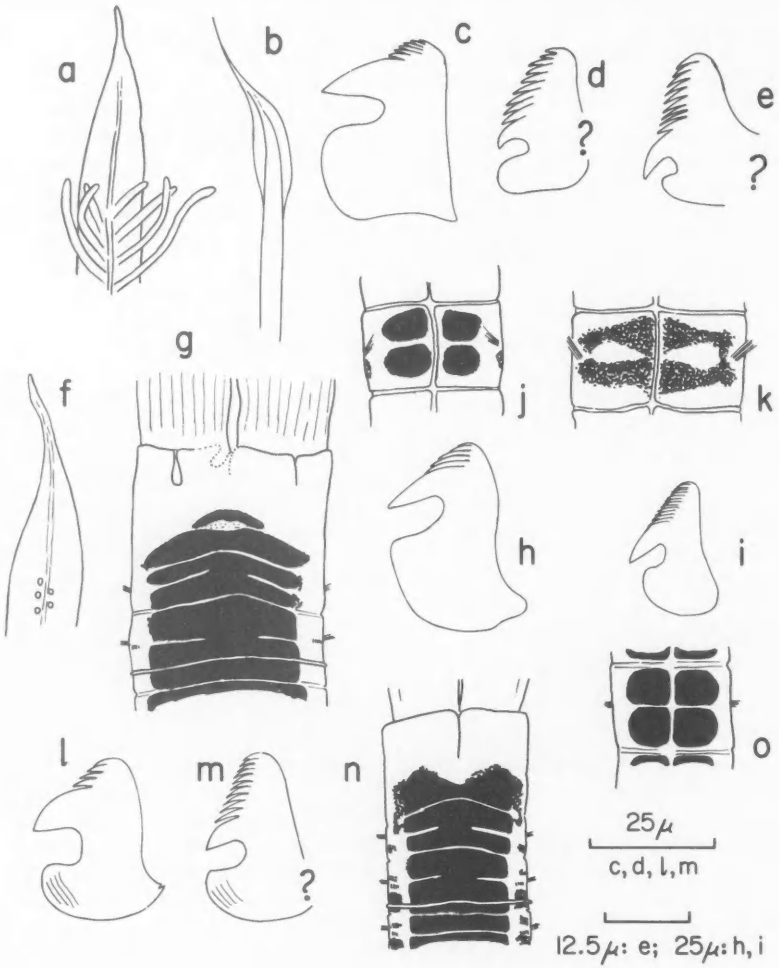

FIGURE 11.—*Euchone elegans*; a, c, d from syntypes, b, e from SEP stn. 2318Ep; a, end of medio-ventral radiole; b, subspatulate notoseta; c, d, middle and dorsalmost uncini from second abdominal setiger; e, uncinus from 17th abdominal setiger (depression); *E. alicaudata*, from holotype: f, end of median radiole; g, ventral view of anterior end of thorax after staining; h, i, uncini from second and 18th abdominal setigers; j, ventral view of middle abdominal segment after staining; k, dorsal view of middle thoracic segment; g, j, and k are oriented in the same way; *E. capensis*, from paratypes: l, m, uncini from second and 19th abdominal setigers, the latter slightly enlarged; n, o, ventral views of anterior end of thorax and median abdominal segment after staining, slightly schematic.

square base similar to those of many other *Chone* and *Euchone* species. The dorsalmost and ontogenetically oldest ones (Figure 11d), have a much higher crown with about 10 rows of teeth and are similar to the uncini in the depression segments (Figure 11e).

After staining with methyl green, the pattern on the first setiger agrees with that of *E. rubrocincta* (cf. Figure 10c) where the incomplete division of the ventral shield reaches somewhat closer to the midline than that of the second one (Figure 10c, marked by x).

Remarks: *Euchone elegans* is close to *E. rubrocincta* from which it is distinguished by the much smaller number of radioles and their short free ends and the form of the uncini of the anterior abdominal segments. The division of the ventral shield at the level of the first parapodium is marked. The species is also similar to *E. analis* as described by Malmgren (1866, 1867; cf. p. 482) but has slightly fewer anterior abdominal setigers. The posterior abdominal uncini of *E. analis* are similar to the anterior ones but are markedly different in *E. elegans*.

EUCHONE ALICAUDATA MOORE AND BUSH

Figure 11f-k

EUCHONE ALICAUDATA Moore and Bush, 1904, p. 165.

Diagnosis: A large *Euchone* species with ventral shields, with 22 abdominal setigers; 8 form anal depression with broad wings. Fifteen to 20 pairs of radioles connected by palmate membrane for one-quarter of their length, with broad flanges extending beyond distal pinnules, and tapering to slender tips. Several pairs of ventral nude filaments. Collar level, with ventro-lateral incisions or folds, probably ventrally incised, concealing the branchial basis. Lower thoracic notosetae subspatulate. Uncini of anterior abdomen with strong necks and bases with posterior extensions; uncini of the posterior abdomen with high crowns.

Material studied: Holotype from 280 m near Tokyo. USNM 5496.

Additions to the Description: The radioles number somewhat more than 15 as stated in the original description; they end in tips as shown in Figure 11f. The collar (Figure 11g) appears to have ventro-lateral incisions rather than folds, as originally stated; owing to injury the presence or absence of a marked midventral incision, implied by Moore and Bush (1904), cannot be verified. A postsetal girdle of glands is present on the second setiger. Bayonet-type setae were not found on the two dissected thoracic notopodia. In this respect, *E. alicaudata* is unique among the 25 species of *Chone* and *Euchone* I have studied; an investigation of more specimens is very desirable. The subspatulate setae were correctly depicted by Moore and Bush (1904, Plate 11, Figure 15). The uncini of the anterior abdomen (Figure 11h) have a posterior extension which is not so distinct in depression segments (Figure 11i). The latter, however, have high crowns with 13 to 15 rows of teeth.

The ventral shields are distinct in thorax and abdomen, becoming even more marked after staining (Figures 11g and 11j). The shields of the first and second setigers are not completely divided by the intrasegmental furrows. The dorsal thoracic staining pattern is shown in Figure 11k. In the abdomen, simple broad bands extend from the level of the parapodia across the dorsum except in the segments of the anal depression where the intrasegmental furrows disappear.

Remark: *Euchone capensis* Day bears some resemblance to *E. alicaudata*, but the species are well distinguished by the form of the ventral shields on the first (buccal) segment (cf. Figures 11g and 11n).

EUCHONE CAPENSIS DAY

Figure 11l-o

EUCHONE CAPENSIS Day, 1961, p. 540; 1967, p. 776.

Diagnosis: A *Euchone* species with ventral shields, with 25 to 32 abdominal setigers; 7 or 8 form anal depression. Nine pairs of radioles,

united by palmate membrane for two-thirds of length, with very long filiform tips. Two to three pairs of ventral nude filaments. Collar approximately as long as branchial basis, with deep ventral incision. Lower thoracic notosetae subspatulate. Uncini of anterior abdomen with strong necks and few rows of teeth, bases with small posterior elongation; uncini of posterior abdomen with greatly enlarged crowns.

Material studied: Paratypes from Stn. TRA. 73M, off South Africa, Ecological Survey, UCT. 311 m. Material at UCT, 3 specimens.

Additions to the Description: The radioles are flanged some distance beyond the palmate membrane. Many pinnules of the middle sections of the radioles extend as far as the end of the distal pinnules. The very long and filiform tips of the radioles extend beyond this level. Whereas Day (1961, Figure 14t; 1967, Figure 37.6j) depicted the branchial base as not concealed by the collar; the branchial base in at least one of the paratypes is hidden. A postsetal girdle of glands is present on the second thoracic setiger. The ventral shields are divided within each thoracic segment. While Day (1961) reported 32 abdominal setigers for the holotype, 2 complete specimens have 25 and 25 or 26 abdominal setigers; 7 or 8 form the anal depression.

An uncinus from the anterior abdominal region is shown in Figure 11l (cf. Day, 1961, Figure 14n). The uncini of the posterior region seem to be similar except that the number of rows of teeth above the main fang is about 10 (Figure 11m). The number of uncini is anteriorly just below, posteriorly slightly above, a dozen per torus.

After using methyl green, the ventral shields are bordered laterally by unstained epidermis (Figure 11n), except in the first thoracic setigers. In the abdomen, intra- and intersegmental borders appear broader than in the thorax, and the outline of the shields becomes rounded (Figure 11q); they are almost circular large patches anterior to the anal depression. Broad, lateral areas of staining cells are present on the first and second thoracic setiger, and a small anterior and a large posterior patch are found around each parapodium on the subsequent segments. These patches seem to be characteristic for the species. The posterior patches tend to form crescents around the parapodia in the abdominal segments. From about the middle part of the abdomen, bands of scattered staining cells cross the dorsal side forming two bands per setiger and becoming most distinct on the depression segments.

Remarks: *Euchone capensis* has abdominal uncini that are somewhat similar to those of *E. alicaudata*, *E. rosea*, and *E. rubrocincta*. The ventral incision in the collar and the distinct abdominal ventral shields separate the South African form clearly from the two latter species. A clear distinction between *E. capensis* and *E. alicaudata* is provided by the form of the ventral shields of the first (buccal) segment (cf. Figures 11g and 11n).

EUCHONE VELIFERA NEW SPECIES

Figure 12

EUCHONE sp. Hartman, 1955, p. 114.

Holotype: Off Catalina Island, Calif., *Velero* station 2412, lat 33°30′02″N, long 118°12′02″W, 593 m, fine mud, 17 Sept. 1953 (cf. Hartman, 1955). AHF, Poly. 0256.

Paratypes: Off Point Vincente Light, Calif., *Velero* station 4854, long 33°47′30″W, lat 118°30′00″W, 179 m, 8 Feb. 1957. AHF Poly. 0453, 2 specimens.

Diagnosis: A large Euchone species with indistinct ventral shields, with 27 to 32 abdominal setigers; 7 to 9 form anal depression with large wings. Nine to 10 pairs of radioles united by palmate membrane for half of their length at least in juveniles, with short filiform free ends. Collar with lateral notches, ventrally deeply incised and folded in between the two halves of the branchial crown, concealing branchial basis. Lower thoracic notosetae subspatulate. Uncini of anterior abdomen with small crowns and square bases; uncini of posterior abdomen with

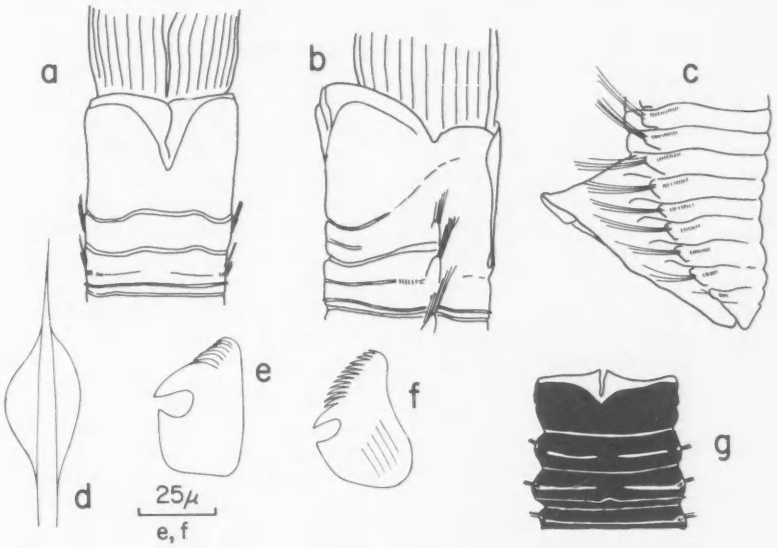

FIGURE 12.—*Euchone velifera* new species; c-e from holotype, a, b from paratypes; a-c, g not drawn to scale: a, b, ventral and left side views of anterior end of juvenile specimen; c, posterior end from the left side; d, subspatulate thoracic seta; e, f, uncini from fifth and 27th (sixth to last) abdominal segments. Accessory teeth schematic; g, anterior end in ventral view showing staining pattern.

high crowns and rounded, posteriorly enlarged bases.

The name refers to the sail-like wings of the anal depression.

Material studied: Type series.

Description: The holotype is a complete, well-preserved mature female of almost 3-cm total length (trunk length 17 mm) and 1.5-mm width. The paratypes are juveniles. In the holotype the branchial crown contributes a little more than one-third of the total length. The 9 or 10 pairs of pinnulated slender radioles are in the holotype free from each other through their entire length and have only rudimentary flanges. The juveniles have a palmate membrane uniting the radioles for approximately half of their length. The pinnules, which are of a uniform, relatively short length, are present almost to the ends of the radioles so that there are only relatively short filiform free tips. A few thin naked filaments are also present, the longest one being about half as long as the radioles. Triangular lips occur on both sides of the mouth.

The collar (Figures 12a and 12b) is slightly longer ventrally than dorsally. The dorsal gap is narrow; laterally there is a small notch. Ventrally, a deep incision is formed by the collar being folded inward between the two halves of the branchial crown. A postsetal girdle of glands encircles the second setiger. The ventral shields of unstained specimens are more distinct in the juveniles than in the adult animal. They are indicated more by the appearance of the ventral and lateral epidermis in the thorax, as contrasted to that of the dorsal side, than by morphological elevation (pads) on the ventrum. This is borne out by staining. In the adult, very conspicuous, subepidermal tissue of a creamy color is present dorsally from the third setiger, having the

appearance of ventral shields. The intrasegmental division of this tissue into anterior and posterior sections is particularly obvious in the abdomen. In contrast to shields, this material is not stained by methyl green. The very large wings of the anal depression are shown in Figure 12c.

Each thoracic notopodium after the first setiger contains three series of setae: about a dozen limbate, about half a dozen bayonet-type setae with very small wings, and 2 doz subspatulate setae (Figure 12d). The thoracic hooks are of the ordinary kind. An uncinus from the anterior abdominal region is shown in Figure 12e; there are about 8 teeth above the main fang in the smaller, and about 10 teeth in the larger, hooks of a torus. Uncini from the posterior regions differ markedly (Figure 12f), not only because of an increase of the number of teeth above the main fang but also by a marked posterior enlargement. There are about half a dozen ventral limbate setae in each abdominal neuropodium with very narrow wings.

The color of the preserved holotype is pale red-brown, except for the dorsal creamy tissue. Very numerous polygonal eggs have diameters up to 150 μ. The tube is clearly constructed by the successive addition of rings of mucus and mud.

After using methyl green, the collar is dorsally fully stained except at the anterior margin; the ventral pattern is indicated in Figure 12g; the patterns on the fourth and following setigers are the same as those on the third. In the abdomen, the intrasegmental divisions appear broader in the thorax so that, owing to the fecal groove, four rectangular fields of pigment per segment are seen. Laterally in the thorax and abdomen, the stained epidermis extends from the shields around the parapodia, uniting immediately dorsal to the notopodia. Staining cells are absent dorsally in the thorax but appear as faint lines in the abdomen.

The two young specimens (paratypes) are about 10 mm long and 0.5 to 0.6 mm wide. The approximately six pairs of radioles are almost as long as the trunk and united by the palmate membrane for about half their length. The collar (Figure 12b) is not as level as in the holotype. The number of abdominal setigers is difficult to ascertain but seems to be 27 or 28 in one, with 7 setigers in the anal depression, and 29 in the other specimen, with 9 setigers in the anal depression.

The smallest uncini in the third and fourth abdominal setiger of one of the specimens were very similar to Figure 12f, that of an uncinus of the adult animal from the posterior segments. The staining pattern is similar to that of the holotype except for a lateral tongue of nonstaining tissue which extends latero-ventrally between the posterior border of the collar, at the level of the lateral notch, and the first parapodium.

Remarks: *Euchone velifera* is unique in regard to its very deeply bilobed collar. Distinct midventral incisions are also known for *E. papillosa* and *E. capensis*. The latter two species lack laterally notched collars and very large wings in the anal depression.

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A MODEL FOR OPTIMAL SALMON MANAGEMENT[1]

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ABSTRACT

Considerable attention has been given in the literature recently to continuous time dynamic maximizing models for fisheries in general, but the time discreteness and interdependency problems encountered in the case of most salmon fisheries have been largely ignored. Hence, a discrete time profit maximizing model for a salmon fishery is developed in this paper, and it is shown that a correct salmon management policy takes the form of an investment decision with respect to the level of escapement and that a management policy of maximum sustained yield may be incorrect from an economic standpoint. It is hoped that continued research including construction of a working model will provide some indication of the difference between the magnitude of spawner stocks selected on the basis of maximum sustained yield and stocks selected on the basis of economic optimality.

Continuous time dynamic maximizing models have been developed in the literature recently to handle the problem of optimally managing a fishery resource (Brown, 1969[3]; Quirk and Smith, 1970[4]). The continuous time approach to analyzing management policy for a salmon fishery tends to be unrealistic since the reproductive process for salmon is periodic, and for certain species reproduction involves rather complex time interdependencies. In the simplest case salmon spawned in a given time period will return to their spawning ground in some future time period, while in more complex cases salmon spawned in a given time period will return to their spawning grounds in several different runs over a number of time periods; also, the level of spawning activity in one time period may affect the fertility of the spawning grounds in future time periods. Such discreteness and time interdependencies cannot be adequately characterized in a continuous time mathematical model.

Hence, the purpose of this paper is to develop a discrete time maximizing model based on currently accepted views of biological spawner-return relationships for salmon; the model is developed with the biological properties of the Bristol Bay fishery foremost in mind (Mathews, 1967). It is shown that a correct fishery management policy takes the form of an investment decision with respect to the level of escapement and that a management policy of maximum sustained yield may be incorrect from an economic standpoint. In essence the fishery manager must decide whether to invest in spawners which yield a return of additional fish at future points in time, or to catch and sell potential spawners today.

In the first section of the paper, the notation and assumptions of the analysis are presented, and in the second section, a simple first-order difference equation model of a salmon fishery is developed and discussed. In the third section, the model is extended to account for the fact that salmon spawned in time period t will return to the spawning grounds in time periods $t+4$, $t+5$, and $t+6$, and also to account for the possibility that fish spawned in time period t will deplete the spawning grounds of food to such an extent that the number of fish the spawning grounds can support in time period $t+1$ will be reduced. Desirable refinements and applications of the model

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[3] Brown, G. W., Jr., 1969. An optimal program for managing common property resource with congestion externalities. Univ. Washington, Seattle. [Mimeograph.]

[4] For a static linear-programming model useful for analyzing fishery management problems see Rothschild and Balsiger, 1971.

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are discussed in the concluding section. In the Appendix the continuous time analog to the simple model is presented.

NOTATION AND ASSUMPTIONS

The notation to be used is as follows:

R_t = the size of a run of salmon into a given river in time period t;
S_t = the number of spawners allowed to escape up the river in time period t;
x_t = the catch of salmon from a given river in time period t;
E_t = the amount of effort used to catch x_t salmon in time period t;
P_E = the price per unit of effort;
P_x = the price per unit of fish;
r = the appropriate discount rate;
T = the total number of years.

The assumptions of the analysis are as follows:

(i) The industry catch for a given river, x_t, is a linear homogeneous function of the amount of effort employed E_t and the size of the run R_t:

$$\begin{aligned} x_t &= F(E_t, R_t) \\ &= R_t F(E_t/R_t, 1) \\ &= R_t f(k_t); \text{ where } k_t = E_t/R_t.^5 \end{aligned}$$

(ii) The biological spawner-return relationship is of the form developed by Ricker (Mathews, 1967):

$$R_t = a S_{t-1} e^{(-bS_{t-1})}.$$

A graph of this function for a simple first order model appears in Figure 1. If a policy of maximum sustained yield is followed, the escapement in year t—1, S^0_{t-1}, occurs where $R_t - S_{t-1}$ is a maximum, or where

$$\frac{d\ (S_{t-1}\ a\ e^{(-bS_{t-1})} - S_{t-1})}{d\ S_{t-1}} =$$

$$a\ e^{(-bS_{t-1})}(1 - b\ S_{t-1}) - 1 = 0.$$

[5] The first derivative of f will be denoted f'.

The escapement in year t is:

$$S_t = R_t - R_t f\ (k_t).$$

(iii) The appropriate objective function to maximize is assumed to be

$$\sum_{t=0}^{T-1} \frac{1}{(1+r)^t}\left[R_t f(k_t)\ P_x - R_t k_t P_E \right] + \frac{1}{(1+r)^T} G(R_T)$$

where the expression on the left is the present worth of industry profits over T—1 years, and the second expression is the present worth of a value function for the terminal stock of fish.

(iv) The price of fish P_x and the price of effort P_E are assumed to remain constant for all time periods.

For some readers the purpose of making these assumptions may at this point appear unclear. Hopefully, the comments to follow will clarify any ambiguities.

In assumption (i) a linear homogeneous aggregate production function is selected for its convenient mathematical properties, and because it has an important economic property, constant returns to scale. In most industry aggregate production function studies, the assumption of constant returns has been found to be reasonably realistic. However, in the case of the salmon industry, this hypothesis has yet to be tested.

The spawner-return relationship specified in assumption (ii) has the usual properties of fishery recruitment functions. It is clear from the graph that spawner stocks to the right of the point $\bar{S}_{t-1}$, where R_t is a maximum as a function of S_{t-1}, are irrelevant from a policy standpoint, since for any feasible run size R_t there corresponds a spawner stock S_{t-1} with $S_{t-1} \leqslant \bar{S}_{t-1}$. Note that no species interaction is implicitly assumed.

The assumption that the present worth of industry profits is the appropriate objective function to maximize is an assumption commonly made in economic analysis. Other types of ob-

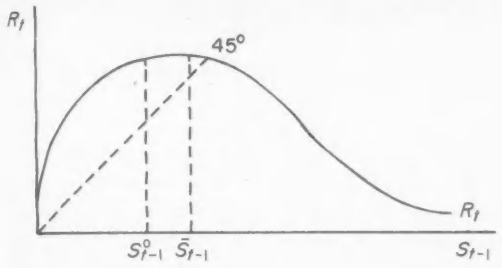

FIGURE 1.—The Ricker spawner-return relationship for salmon.

jective functions are mathematically feasible, but it is not obvious what they might be without going beyond the scope of this paper and undertaking a political analysis of salmon fishery management. Specifying a terminal value function is a mathematical necessity and will be discussed later.

Assumption (iv) implies, among other things, that the catch x_t from the salmon stock being analyzed is not large enough to influence the total industry price structure for salmon and that the factor supply market for effort, E_t, is competitive.

The problem of gear congestion on the fishing ground is adequately dealt with elsewhere and is avoided here by assuming that the fishery management authority undertakes appropriate policies to insure that only efficient levels of effort are employed (see footnote 3; Quirk and Smith, 1970). It is also assumed that salmon are not caught on the high seas but are harvested as they return to the river to spawn.

A SIMPLE MODEL

In this section the simplest type of spawner-return relationship is examined where salmon spawned in time period t—1 return to their spawning ground in time period t. Given the assumptions of the above section, the problem is to maximize

$$\sum_{0}^{T-1} \frac{1}{(1+r)^t}\left(R_t f(k_t) P_x - R_t k_t P_E\right) + \frac{1}{(1+r)^T} G(R_T),$$

subject to:

$$S_t = R_t - R_t f(k_t), S_t \geqslant 0, k_t \geqslant 0, R(0) = R_0,$$

and

$$R_t = a S_{t-1} e^{(-bS_{t-1})}.$$

The appropriate Lagrangian for the maximization problem is:

$$L(k, S, \lambda) = \sum_{0}^{T-1} \frac{1}{(1+r)^t}\left(R_t (P_x f(k_t) - P_E k_t)\right) + \frac{1}{(1+r)^T} G(R_T) + \sum_{0}^{T-1} \frac{1}{(1+r)^t} \lambda_t [R_t - R_t f(k_t) - S_t], \quad [1]$$

where $k = (k_0, \ldots, k_{T-1})$, $S = (S_0, \ldots, S_{T-1})$, and $\lambda = (\lambda_0, \ldots, \lambda_{T-1})$, and R_0 is given.

The appropriate Kuhn-Tucker necessary conditions for a maximum of $L(k, S, \lambda)$ are as follows:

$$\partial L/\partial k_t \leqslant 0; k_t \partial L/\partial k_t = 0, \quad t = 0, \ldots, T-1; \quad [2]$$

$$\partial L/\partial S_t \leqslant 0; S_t \partial L/\partial S_t = 0, \quad t = 0, \ldots, T-1; \quad [3]$$

$$\partial L/\partial \lambda_t = 0, \quad t = 0, \ldots, T-1. \quad [4]$$

It is assumed that the solution to the maximizing problem is interior; i.e., $k_t > 0, S_t > 0, \lambda_t > 0$. Then [2] and [3] are satisfied if [5], [6], and [7] are true:

$$(P_x - \lambda_t)\, f'(k_t) = P_E, \quad t = 0, \ldots, T-1; \quad [5]$$

$$\lambda_{t-1} = \frac{1}{(1+r)} \left(P_x\, f(k_t) - P_E\, k_t\right) dR_t/dS_{t-1} + \frac{1}{(1+r)}\, \lambda_t\, [1 - f(k_t)]\, dR_t/dS_{t-1},$$

$$t = 1, \ldots, T-1; \quad [6]$$

$$\lambda_{T-1} = \frac{1}{(1+r)} \frac{dG}{dR_T} \frac{dR_T}{dS_{T-1}}, \quad [7]$$

and [4] is satisfied if [8] is true.

$$S_t = R_t - R_t\, f(k_t), \quad t = 0, \ldots, T-1. \quad [8]$$

For $t = 1$ equation [6] can be written more simply as

$$\lambda_0 = \frac{1}{1+r}[P_x\, f(k_1) - P_E\, k_1] \frac{dR_1}{dS_0} + \frac{1}{1+r}\, \lambda_1 \frac{\partial S_1}{\partial S_0}. \quad [6']$$

By substituting for λ_1 in [6'], an expression of λ_0 results with λ_2 in it, and by substituting for λ_2 an expression of λ_0 results with λ_3 in it, and so on until an expression of λ_0 results with λ_{T-1} in it. Equation [7] can then be substituted for λ_{T-1}.[6] The resulting expression is:

$$\lambda_0 = \sum_{t=1}^{T-1} \frac{1}{(1+r)^t} \left[P_x\, f(k_t) - P_E\, k_t\right] \frac{\partial R_t}{\partial S_0} + \frac{1}{(1+r)^T} \frac{dG}{dR_T} \frac{\partial R_T}{\partial S_0}. \quad [9]$$

Equation [5] can be rewritten for $t = 1$ as

$$\lambda_0 = P_x - P_E/f'(k_0). \quad [5']$$

Equation [5'] suggests that λ_0 can be interpreted as the marginal profitability of catching an additional fish in period 0, while equation [9] suggests that λ_0 can be interpreted as the present value of the marginal profitability of adding an additional spawner to the escapement level in period 0; i.e., the level of escapement should be selected in time period 0 such that the incremental profitability of an additional fish caught today is just equal to the present value of the profitability of the future return resulting from an incremental spawner. In order to attain the desired level of escapement it is necessary to select an appropriate level of k_0, since escapement is equal to the run size in period 0 minus the catch. Note that this analysis can be applied to any time period t, not just to $t = 0$.

In order for the analysis to be valid in the general form presented here, it is necessary to prove the existence of values for $k = (k_0, \ldots, k_{T-1})$, $S = (S_0, \ldots, S_{T-1})$, and $\lambda = (\lambda_0, \ldots, \lambda_{T-1})$, which satisfy equations [5], [6], [7], and [8] given $R_0 = R(0)$. This is not an easy task if T is finite, so it is assumed that $T \to \infty$.[7] In this situation an equilibrium, or steady state solution is possible, where

$$k^* = k_0 = k_1 = \ldots, = k_T$$

$$S^* = S_0 = S_1 = \ldots, = S_T$$

$$\lambda^* = \lambda_0 = \lambda_1 = \ldots, = \lambda_T.$$

If T is finite this kind of a solution makes no sense. If $T \to \infty$ and an equilibrium solution exists, then equation [9] can be rewritten as

[6] This procedure is discussed in Burt and Cummings (1970).

[7] For a discussion of the mathematical problems involved in the case of an infinite time horizon (Burt and Cummings, 1970).

$$\lambda^* = \sum_{t=1}^{\infty} \frac{1}{(1+r)^t} [P_x f(k^*) - P_E k^*] \frac{\partial R_t^*}{\partial S_0} + \lim_{T \to \infty} \frac{1}{(1+r)^T} \frac{dG}{dR_T} \frac{\partial R_T^*}{\partial S_0}.^{8} \quad [9']$$

Both expressions to the right of the equal sign in equation [9′] must converge for existence. This requires that

$$\frac{dR^*}{dS} [1 - f(k^*)] < 1 + r. \quad [10]$$

Then equation [9′] can be rewritten as

$$\lambda^* = \frac{1}{1+r} [P_x f(k^*) - P_E k^*] \frac{dR^*}{dS} \cdot \frac{1}{1 - \frac{[1-f(k^*)]}{1+r} \frac{dR^*}{dS}} \quad [9'']$$

since $\lim_{T \to \infty} \frac{1}{(1+r)^T} \frac{dG}{dR_T} \frac{\partial R_T^*}{\partial S_0}$ converges to zero for $\frac{dG}{dR_T}$ bounded. Also [5] and [8] can be rewritten as

$$(P_x - \lambda^*) f'(k^*) = P_E, \quad [5']$$

$$S^* = R^* - R^* f(k^*). \quad [8']$$

Equations [10] and [9″] together suggest that the productivity of the spawner stock in producing additional spawners must be less than the social rate of discount, r, in order for λ^*, the profitability of an incremental spawner, to be positive.

A steady state solution exists if the determinant of the Jacobian matrix for [5′], [8′], and [9″], is non-zero. It can be proven that the Jacobian determinant is negative if it is assumed that the expression to the left of the inequality sign in [10] is less than or equal to 1. Unfortunately, there is no reason to assume this, even though in the context of a specific model, with functions and parameters assigned, one might expect that it is true.[9]

Note that the equilibrium solution requires that $R_0 = S^*/(1 - f(k^*))$. Clearly there is no reason to anticipate that the initial run size will be at the desired level for an equilibrium solution, and to reach the desired level may be costly. Hence, the analysis ignores the question of optimal policy for reaching the equilibrium solution. Note also that there is no reason to anticipate that S^*, the equilibrium solution, will correspond to maximum sustained yield. These issues are discussed more extensively in the appendix in the context of a continuous time model.

MORE COMPLEX MODELS

A simple model of the type presented in the previous section is not completely realistic for certain species of salmon where fish spawned in time period t will return to their spawning grounds in time periods $t+4$, $t+5$, and $t+6$. Assuming that the percentages of the total return to the river in time periods $t+4$, $t+5$, and $t+6$ from spawning efforts in time period t are constants, a_4, a_5, and a_6, the spawner-return relationship becomes:

$$R_t = S_{t-4} a_4 a e^{(bS_{t-4})} + S_{t-5} a_5 a e^{(-bS_{t-5})} + S_{t-6} a_6 a e^{(-bS_{t-6})}, \quad [11]$$

where $a_4 + a_5 + a_6 = 1$.

[8] In a steady state solution,

$$\frac{\partial R_t}{\partial S_0} = \frac{dR^*}{dS} \left([1 - f(k^*)] \frac{dR^*}{dS} \right)^{t-1}$$

where * denotes evaluation at the equilibrium solution. Note also that

$$\frac{\partial R_t}{\partial S_1} = \frac{dR_t}{dS_{t-1}} \prod_{\tau=1}^{t-1} [1 - f(k_\tau)] \frac{dR_T}{dS_{T-1}} = \frac{dR_t}{dS_{t-1}} \prod_{\tau=1}^{t-1} \frac{\partial S_\tau}{\partial S_{\tau-1}}$$ in the general case.

[9] See the appendix for a proof that the Jacobian determinant is negative for the given assumption.

The Lagrangian for the maximizing problem now becomes:

$$L = \sum_{t=0}^{T-6} \frac{1}{(1+r)^t} \Big(R_t \left[P_x f(k_t) - P_E k_t \right] + \lambda_t \left[R_t - R_t f(k_t) - S_t \right] \Big) + \sum_{t=T-5}^{T} \frac{1}{(1+r)^t} G(R_t), \quad [12]$$

given $R(0) = R_0$, $R(1) = R_1$, $R(2) = R_2$, $R(3) = R_3$, $R(4) = R_4$, and $R(5) = R_5$. Note that in this model R_0, R_1, R_2, R_3, R_4, and R_5 are the given initial run sizes and that the terminal value condition must be modified to account for the more complex spawner-return relationship now being used. Also, it is implicitly assumed that run sizes in the last five periods have no direct effect on one another, but are determined by spawner stocks in previous periods. Once $T \to \infty$ is allowed this assumption becomes unimportant.

The necessary conditions for a maximum of L with $k_t > 0$, $S_t > 0$, $\lambda_t > 0$ are satisfied if:

$$(P_x - \lambda_t) f'(k_t) = P_E, \quad t = 0, \ldots, T-6; \quad [13]$$

$$\lambda_{t-4} = \frac{1}{(1+r)^4} \Big(\left[P_x f(k_t) - P_E k_t \right] + \lambda_t \left[1 - f(k_t) \right] \Big) \frac{\partial R_t}{\partial S_{t-4}} + \frac{1}{(1+r)^5} \Big(\left[P_x f(k_{t+1}) - P_E k_{t+1} \right] + \lambda_{t-1} \left[1 - f(k_{t+1}) \right] \Big) \frac{\partial R_{t+1}}{\partial S_{t-4}} + \frac{1}{(1+r)^6} \Big(\left[P_x f(k_{t+2}) - P_E k_{t+2} \right] + \lambda_{t-2} \left[1 - f(k_{t+2}) \right] \Big) \frac{\partial R_{t+2}}{\partial S_{t-4}},$$

$$t = 4, \ldots, T-8; \quad [14]$$

$$\lambda_{T-11} = \frac{1}{(1+r)^4} \Big(\left[P_x f(k_{T-7}) - P_E k_{T-7} \right] + \lambda_{T-7} \left[1 - f(k_{T-7}) \right] \Big) \frac{\partial R_{T-7}}{\partial S_{T-11}} + \frac{1}{(1+r)^5} \Big(\left[P_x f(k_{T-6}) - P_E k_{T-6} \right] + \lambda_{T-6} \left[1 - f(k_{T-6}) \right] \Big) \frac{\partial R_{T-6}}{\partial R_{T-11}} + \frac{1}{(1+r)^6} \frac{dG}{dR_{T-5}} \frac{\partial R_{T-5}}{\partial S_{T-11}}; \quad [15]$$

$$\lambda_{T-10} = \frac{1}{(1+r)^4} \Big(\left[P_x f(k_{T-6}) - P_E k_{T-6} \right] + \lambda_{T-6} \left[1 - f(k_{T-6}) \right] \Big) \frac{\partial R_{T-6}}{\partial S_{T-10}} + \frac{1}{(1+r)^5} \frac{dG}{dR_{T-5}} \frac{\partial R_{T-5}}{\partial S_{T-10}} + \frac{1}{(1+r)^6} \frac{dG}{dR_{T-4}} \frac{\partial R_{T-4}}{\partial S_{T-10}}; \quad [16]$$

$$\lambda_{T-9} = \frac{1}{(1+r)^4} \frac{dG}{dR_{T-5}} \frac{\partial R_{T-5}}{\partial S_{T-9}} + \frac{1}{(1+r)^5} \frac{dG}{dR_{T-4}} \frac{\partial R_{T-4}}{\partial S_{T-9}} + \frac{1}{(1+r)^6} \frac{dG}{dR_{T-3}} \frac{\partial R_{T-3}}{\partial S_{T-9}}; \quad [17]$$

$$\lambda_{T-8} = \frac{1}{(1+r)^4} \frac{dG}{dR_{T-4}} \frac{\partial R_{T-4}}{\partial S_{T-8}} + \frac{1}{(1+r)^5} \frac{dG}{dR_{T-3}} \frac{\partial R_{T-3}}{\partial S_{T-8}} + \frac{1}{(1+r)^6} \frac{dG}{dR_{T-2}} \frac{\partial R_{T-2}}{\partial S_{T-8}}; \quad [18]$$

$$\lambda_{T-7} = \frac{1}{(1+r)^4} \frac{dG}{dR_{T-3}} \frac{\partial R_{T-3}}{\partial S_{T-7}} + \frac{1}{(1+r)^5} \frac{dG}{dR_{T-2}} \frac{\partial R_{T-2}}{\partial S_{T-7}}$$

$$+\frac{1}{(1+r)^6}\frac{dG}{dR_{T-1}}\frac{\partial R_{T-1}}{\partial S_{T-7}}\ ; \qquad [19]$$

$$\lambda_{T-6} = \frac{1}{(1+r)^4}\frac{dG}{dR_{T-2}}\frac{\partial R_{T-2}}{\partial S_{T-6}} + \frac{1}{(1+r)^5}\frac{dG}{dR_{T-1}}\frac{\partial R_{T-1}}{\partial S_{T-6}} + \frac{1}{(1+r)^6}\frac{dG}{dR_T}\frac{\partial R_T}{\partial S_{T-6}}\ ; \qquad [20]$$

$$S_t = R_t\,[1-f(k_t)],\ t=0,\ldots,T-6. \qquad [21]$$

For a steady state (k^*, S^*, λ^*) these necessary conditions reduce to the following:

$$(P_x-\lambda^*)\,f'(k^*) = P_E, \qquad [22]$$

$$\lambda^* = [P_x f(k^*) - P_E k^*]\,\frac{dR^*}{dS} \times \frac{D}{1-D\,[1-f(k^*)]\frac{dR^*}{dS}} \qquad [23]$$

$$S^* = R^*\,[1-f(k^*)], \qquad [24]$$

where $D = \frac{a_4}{(1+r)^4}+\frac{a_5}{(1+r)^5}+\frac{a_6}{(1+r)^6}$.

In order for λ^* to be positive, $[1-f(k^*)]\,\frac{dR^*}{dS}$ must be less than $1/D$. The economic interpretations of [22], [23], and [24] are the same as the corresponding interpretations of [5′], [9″], and [8′] in the second section.

Some biologists believe that for certain species and spawning grounds spawned salmon in time period t will deplete the spawning grounds of food to such a degree that food sources will not be replenished sufficiently in time period $t+1$ to support an equally large number of spawned fish. The nature of this phenomenon has not yet been very well specified, but one possible expression of it is the following spawner-return relationship where feeding interaction between years is accounted for by modification of the power term for e:

$$R_t = S_{t-4}\,a_4 a e^{(-b_1 S_{t-4} - b_2 S_{t-5})} + S_{t-5}\,a_5 a e^{(-b_1 S_{t-5} - b_2 S_{t-6})} + S_{t-6}\,a_6 a e^{(-b_1 S_{t-6} - b_2 S_{t-7})}\ . \qquad [25]$$

The necessary conditions in a steady state for the model using this spawner-return relationship are the same as [22], [23], and [24], except that $\frac{dR^*}{dS}$ must be replaced by $\frac{dR^*}{dS} = a e^{-(b_1+b_2)S^*}\,(1-b_1 S^* - \frac{b_2}{1+r}\,S^*)$.

One thing should be noted about the two models presented in this section. In order to attain the steady state solution, it is necessary to set the run size equal to its equilibrium solution level for the first six periods in the first model and the first seven periods in the second model. Hence, the problem of attaining the equilibrium solution is of greater magnitude here than in the simple model, where it was necessary to set the run size equal to its equilibrium solution level only in the initial period. This problem can, perhaps, be more adequately dealt with in the framework of a specific model and, in any case, requires further research.

NEEDED REFINEMENTS

Thus far, the analysis considers only necessary conditions for the existence of a maximizing solution. Sufficient conditions for existence are satisfied if the Lagrangian is concave in all variables. Unfortunately, concavity neither can be proved or disproved for the models examined in this paper. Again, the proof may be possible in the context of a more specific model, where all parameters and functions are assigned.

A practical application of the model presented here would involve significantly difficult estimation problems. Some work has already been done on estimating spawner-return functions, but the results in most cases have not been too promising (Mathews, 1967). The spawner-re-

turn relationships seem to possess a high degree of variability, which suggests that a stochastic specification of the problem may be more realistic than our deterministic approach. Estimating a catch function may also be troublesome since it would require a careful specification of effort and of its price.

Despite the difficulties, construction of a working model would be worthwhile because it would provide insight into some of the unresolved mathematical problems mentioned above, and more importantly it would provide further information on the significance of the difference between the magnitude of spawner stocks selected on the basis of maximum sustained yield and stocks selected on the basis of economic optimality as defined in this paper.

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APPENDIX

A continuous time analog to the simple model will now be discussed briefly. The problem is to maximize.

$$\int_0^\infty R_t[P_x f(k_t) - P_E k_t] e^{-\rho t} dt \qquad [A\text{-}1]$$

subject to

$$\dot{S}_t = R_t[1 - f(k_t)] - S_t, \qquad [A\text{-}2]$$

where $\dot{S}_t = \frac{dS_t}{dt}$, and ρ is the continuous time discount rate. The appropriate Hamiltonian for the maximum problem is

$$H = e^{-\rho t}\Big(R_t[P_x f(k_t) - P_E k_t] + \lambda_t[R_t[1\text{-}f(k_t)] - S_t - \dot{S}_t]\Big). \qquad [A\text{-}3]$$

Assuming the existence of an interior solution, the necessary conditions for a maximum are, along with [A-2],

$$\frac{\partial H}{\partial k_t} = 0, \qquad [A\text{-}4]$$

$$\frac{d}{dt}\frac{\partial H}{\partial \dot{S}_t} = \frac{\partial H}{\partial S_t}. \qquad [A\text{-}5]$$

[A-4] and [A-5] are satisfied if

$$(P_x - \lambda_t) f' = P_E, \qquad [A\text{-}4']$$

$$\dot{\lambda}_t = \rho\lambda_t - \Big([P_x f(k_t) - P_E k_t]\frac{dR_t}{dS_t} + \lambda_t[1 - f(k_t)]\frac{dR_t}{dS_t} - \lambda_t\Big) \qquad [A\text{-}5']$$

where $\dot{\lambda}_t = d\lambda/dt$.

If [A-4'] is used to eliminate one of the unknowns, the result is a system of two differential equations in two unknowns, [A-2] and

[A-5']. Utilizing the following derivatives, it is possible to consider a phase diagram analysis of this equation system.

$$d\lambda_t/dS_t \Big|_{\dot{\lambda} = 0} =$$

$$+\left(\frac{[P_x f(k_t) - P_E k_t] + \lambda_t[1 - f(k_t)]}{\rho + 1 - [1 - f(k_t)]\, dR_t/dS_t} \right) \frac{d^2R_t}{dS_t^2} \qquad \text{[A-6]}$$

$$d\lambda_t/dS_t \Big|_{\dot{S} = 0} =$$

$$\frac{(P_x - \lambda_t) f'' \left([1 - f(k_t)] \frac{dR_t}{dS_t} - 1 \right)}{R_t f'^2}, \qquad \text{[A-7]}$$

$$\frac{\dot{d\lambda}}{dS_t} \Big|_{\lambda \text{ constant}} =$$

$$-\left([P_x f(k_t) - P_E k_t] + \lambda_t[1 - f(k_t)] \right) \frac{d^2R_t}{dS_t^2}, \qquad \text{[A-8]}$$

$$\frac{\dot{dS}}{d\lambda_t} \Big|_{S_t \text{ constant}} = -\frac{R_t f'(k_t^2)}{(P_x - \lambda_t) f''(k_t)}. \qquad \text{[A-9]}$$

Before proceeding with the analysis, note that:

(i) $f' > 0, f'' < 0, P_x - \lambda_t > 0$ by [A-4'], and $[(P_x - \lambda_t) f(k_t) - P_E k_t + \lambda_t] > 0$ since $P_x - \lambda_t = P_E/f'$ and $f > f' k_t$.

(ii) If a steady state solution exists, such that $\dot{\lambda}_t = 0$ and $\dot{S}_t = 0$, which satisfies the necessary conditions for a maximum, the equilibrium value for S_t, S^*, will be such that $S^* \leqslant \bar{S}_t$ where $\bar{S}_t$ maximizes R_t as a function of S_t. The reason for this was discussed in the section on Notation and Assumptions. It then follows that $dR_t/dS_t > 0$, and $d^2R_t/dS_t^2 < 0$.

(iii) $0 < [1 - f(k_t)] \leqslant 1$ since $S_t = R_t\,[1 - f(k_t)] \geqslant 0$ and $S_t \leqslant R_t$.

(iv) $dR_t/dS_t = 1$ evaluated at S_t^0, where S_t^0 is the spawner stock required for maximum sustained yield; if $S_t < S_t^0$, $dR_t/dS_t > 1$, and if $S_t > S_t^0$, $dR_t/dS_t < 1$.

It is now possible to attach signs to [A-6] through [A-8] as follows:

$$d\lambda_t/dS_t \Big|_{\dot{\lambda} = 0} < 0 \text{ for } S_t^0 \leqslant S_t \leqslant \bar{S}_t, \qquad \text{[A-10]}$$

indeterminant for $S_t < S_t^0$;

$$d\lambda_t/dS_t \Big|_{\dot{S} = 0} > 0 \text{ for } S_t^0 \leqslant S_t \leqslant \bar{S}_t, \qquad \text{[A-11]}$$

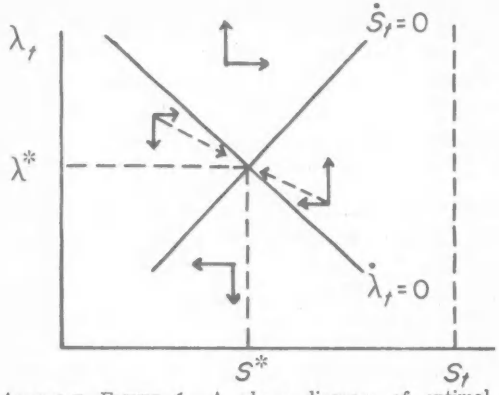
interminant for $S_t < S_t^0$;

$$\frac{\dot{d\lambda}}{dS_t} \Big|_{\lambda \text{ constant}} > 0 \text{ for } S_t \leqslant S_t. \qquad \text{[A-12]}$$

$$\frac{\dot{dS}}{d\lambda_t} \Big|_{S_t \text{ constant}} > 0, \ \forall\ S_t. \qquad \text{[A-13]}$$

If $[1 - f(k_t)]\, \frac{dR_t}{dS_t} \leqslant 1$, then there are no sign ambiguities in the relevant range, and the equilibrium solution exists. From the phase diagram in Appendix Figure 1, it is clear that the equilibrium is a saddle point; i.e., given an initial $S_0 \leqslant \bar{S}_t$, there exists a time path for λ_t, k_t, and S_t converging to the steady state equilibrium, along which the necessary conditions for a maximum are satisfied. Hence, the optimal policy for reaching a steady state solution can be specified even if $S_0 \neq S^*$. Again there is no reason for $S^* = S_t^0$, where S_t^0 corresponds to maximum sustained yield.

It is now possible to calculate the Jacobian determinant J of the system of equations [A-2] and [A-5'] evaluated at the steady state equilibrium, using [A-4'] to eliminate one of the variables. In order to calculate the determinant, the following derivatives are required:



APPENDIX FIGURE 1.—A phase diagram of optimal solution paths.

$$\frac{\partial \dot{\lambda}_t}{\partial \lambda_t} = \rho + 1 - [1 - f(k_t)]\, dR_t/dS_t, \quad \text{[A-14]}$$

$$\partial \dot{S}_t/\partial S_t = \frac{dR_t}{dS_t} 1 - f(k_t)] - 1. \quad \text{[A-15]}$$

Using [A-8], [A-9], [A-14], and [A-15], and assuming that $[1 - f(k_t)]\, \frac{dR_t}{dS_t} \leqslant 1$,

$$J = \begin{vmatrix} \frac{\partial \dot{\lambda}_t}{\partial \lambda_t} & \frac{\partial \dot{\lambda}_t}{\partial S_t} \\ \frac{\partial \dot{S}_t}{\partial \lambda_t} & \frac{\partial \dot{S}_t}{\partial S_t} \end{vmatrix} < 0.$$

If r is substituted for ρ in the determinant, it equivalent to the one discussed in the second section.

As in the second section, it is not possible to prove that the equilibrium solution satisfies sufficient conditions for a maximum, since, in this case, it is not possible either to prove or disprove the concavity of the Hamiltonian.

NOTES

A SECOND RECORD OF A RARE SIPHONOPHORE *EPIBULIA RITTERIANA* HAECKEL 1888

During a survey by the National Marine Fisheries Service research vessel *David Starr Jordan*, a siphonophore, *Epibulia ritteriana* Haeckel, of the family Epibuliidae, was collected in a neuston haul on July 10, 1971, at 0225 to 0246 hr, PST, in the northeast Pacific Ocean at lat 37°20'N, long 135°00'W. The only other record of this species was one specimen, described by Haeckel (1888), collected off Ceylon in 1882 during the *Challenger* Expedition. Evidence of the worldwide distribution is typical of most species of siphonophores.

Haeckel's identification was refuted by Totton and Bargmann (1965) who stated several reasons for their disagreement, the most important being that Haeckel had described a ring of palpons under the float which they said was a character not typical of the suborder Cystonectae. Totton and Bargmann (1965) stated further that the suborder included only the families Physalidae and Rhizophysidae; the Epibuliidae were considered "species inquirendae." They concluded that Haeckel's description was based on "an incompletely examined specimen of *Athorybia rosacea*," and "that Haeckel's figure is unrealistic and idealized though beautifully executed," and in their opinion, "if such animals existed no doubt one will be found again." They also disagreed with unillustrated descriptions of two species of Epibuliidae, one *Rhyzophysa chamissomis* by Eysenhardt (1821) and the other *Epibulia erythrophysa* by Brandt (1835). It was my good fortune to collect and observe the living cystonect, described and illustrated here, which I have identified as *E. ritteriana* by reference to Haeckel's drawings and description. Haeckel's specimen is identical with mine, except that the gastrozoids in his illustration have larger and more conspicuous mouths. I have also collected specimens of *Athorybia rosacea*, identified by direct observation and comparison with drawings by Totton and Bargmann (1965). Outstanding characters of *A. rosacea* are the shape of the pneumatophore and large and distinct bracts arranged in several layers. My specimen of *E. ritteriana* showed no evidence of bracts, nor scars or spaces where bracts could be attached. I believe, therefore, that the two species are not to be confused and that *Epibulia* does in fact exist, *ergo*, the family Epibuliidae.

The rarity of records for this family of cystonects may be attributed in part to the fact that as surface floating organisms they exist in a stratum seldom sampled by plankton tows because most "net time" is subsurface.

Description of *Epibulia ritteriana*

The complete corm of this Cystonectae is about 25 mm high and 20 mm in diameter, after preserved in 5% solution of formaldehyde (Figure 1). The whole colony presented brilliant shades of pink. The large ovate, almost spheric pneumatophore was coral red (light red) with the apical pore (with a sphincter) surrounded by a purple pigmentation, still visible after preservation. The crown of palpons around the float (young gastrozoids) and the siphons (gastrozoids) appeared rose, and the latter presented a purple spot near the end. Tentacles and tentilla were yellowish, the gonodendra bright red and purple.

The colony appears arranged as follows: pneumatophore and siphosome. The siphosome presents the palpons at the part closer to the pneumatophore, and the siphons at the other end, with the tentacles attached at the base; and the gonodendra distributed between the siphons.

The pneumatophore or top float is filled with gas, probably carbon monoxide as it is the case in other siphonophores (Pickwell, Barham, and Wilton, 1964). The pneumatophore is an ovate chitinous case, 8 mm × 10 mm in size. According to Haeckel (1888) the size of the pneumatophore ranged from 10 mm × 12 mm in the expanded stage to a spheroid of 3 to 4 mm after

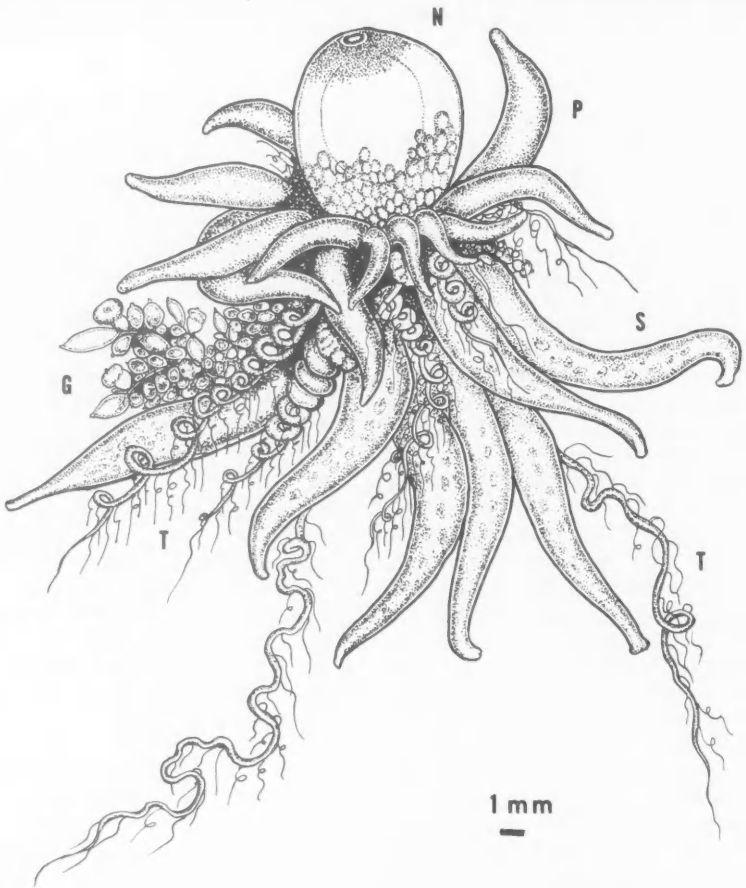


FIGURE 1.—*Epibulia ritteriana* Haeckel (1888), drawn from the specimen described in this paper. Key to the above is: N - pneumatophore, P - palpons, S - siphons or gastrozoids, T - tentacles with the tentilla, G - gonodendra.

the emission of the gas through the apical pore. The structure of the pneumatophore, according to Haeckel (1888) includes the pneumatocodon or outer wall of the pneumatophore, which is separated from the inner wall, or pneumatosac, pneumatocyst or air sac, which contains the gas gland; and the hypocystic villi (giant cells) protrude from the air sac into the pericystic space. The apical pore is closed by the stigmatis sphicter (ring muscle).

The siphosome is a short cone or ovate bladder, coiled, which Haeckel (1888) described as the "dexiotropic turning of a spire."

The palpons (feelers or testers) are slender, cylindrical tubes, smaller than the siphons, with a thick muscular wall. They connect into the vascular trunk, and the outer end is armed with cnidocysts. The palpons are consequently then both sensory and protective organs.

The siphons or gastrozoids are large feeding polyps, 15 mm to 20 mm long, rod-shaped tubes of thick muscular wall. The largest part is the stomach with the hepatic villi, and the outer opening a muscular proboscis. The opening of the mouth may be expanded in a kind of disc or sucker, divided into several lobes. Haeckel's illustrations (1888) presented the gastrozoids with extremely large and expanded mouth. A long single contractile tentacle is attached at the base of each siphon.

The tentacle arising from the base of each gastrozoid consists of a long cylindrical tube reaching to 80 mm or more than 100 mm long when fully extended. The tentacles are long, contractile, and branched along their whole length, which is covered laterally by the single branched tentilla. The tentilla are short, thin, contractile filaments. Both tentacles and tentilla are covered with nematocysts. The concave side of each tentillum has sensitive papillae, and the convex side is armed with cnidocysts. Twisted masses of tentacles and tentilla form thick bunches, difficult to disentangle.

The gonodendra are attached by a short pedicle to the periphery of the vesicular trunk, between the palpons and the siphons or gastrozoids. The gonostyle is branched, and each branch has at the end a gonopalpo and a medusoid gynophore (female gonophore) and below a bunch of roundish androphores (male gonophores) resembling altogether miniature clusters of grapes.

Epibuliidae float at the surface of the waters, using the pneumatophore, swimming mainly by the coordinated movements of the palpons, and siphons. *E. ritteriana* adopts a vertical position in the water, and the colony drifts and twists at the surface of the sea, with the pneumatophore at the top, floating at the surface, and the tentacles shortened or extended deep into the waters like fishing lines, with the gastrozoids actively searching for food.

It is possible that *Cystalia monogastrica* Haeckel (1888) may be a juvenile stage of *Epibulia ritteriana.*

The scarcity of *E. ritteriana* is probably only apparent, due to the factors previously explained. Studies on the distribution of these highly predatory animals would be of interest, when related to the distribution of some fish larvae. These Cystonectae may feed voraciously on epiplanktonic animals, mainly on those inhabiting the uppermost layers of the epiplanktonic domain (Clupeidae, Engraulidae, and other fish larvae), which would suffer heavily under this active predation.

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DEEP OBSERVATIONS OF ANCHOVY AND BLUE SHARKS FROM *DEEPSTAR 4000*

Visual observations from manned deep-submersibles have recently contributed to the knowledge of the vertical distribution of marine organisms. Prior to the introduction of these craft, vertical distribution patterns were established using sampling gear such as nets. This was generally sufficient in the case of the smaller, easily captured forms since many of the nets used in these studies could be opened and closed at predetermined depths so that selected strata would be sampled exclusively. In the case of the larger, more active fishes, however, knowledge of their depth ranges has been mostly speculative. Sampling of these animals has normally been accomplished using commercial fishing gear which is generally indiscriminate with respect to the depth of capture. This has been true of the two species in question, the northern anchovy, *Engraulis mordax* Girard, and the blue shark, *Prionace glauca* (Linnaeus).

One method used to establish the depth of anchovy schools has been to locate them with echo sounders during the day when they are deep, then remain over them until they rise to the surface at night. Once the schools are at the surface, identification can be made with midwater trawls. Common daytime depths of these schools are between 140 and 220 m (personal communication with K. F. Mais, California Department of Fish and Game). Information on vertical distribution of blue sharks has been reported by Strasburg (1958). Analysis of longline fishing data from the central Pacific showed that these sharks were often captured on the deepest hooks. Although the exact depth of the hooks at the time of capture was not known, the approximate depths were in the 110-150 m range. This report, then, should serve as a visual verification of this previous information.

Dive 502 of the submersible *Deepstar 4000* was made on 9 November 1968 at lat 32°26′N, long 117°23′W, west of the Coronado Islands. On the way to the dive site from San Diego aboard the mothership *Searchtide*, a continuous echogram was made on a Gifft GDR-T depth recorder[1] driving a hull-mounted UQN-1 transducer at 12 kHz. Shortly after cresting the Coronado Escarpment, where the bottom dropped off to the deeper water of the San Diego Trough, hyperbolic targets appeared in the 160 to 270 m region of the recording. Underway at 12 knots, the largest of these had dimensions of 600 m horizontally, and 70 m vertically. As *Searchtide* hove-to at the dive site, these targets appeared as in Figure 1. Interspersed with the large targets were several discrete targets which appear on the record as lines, rather than large masses. The bottom depth at the site was approximately 1,200 m and its trace was programmed out of the recording.

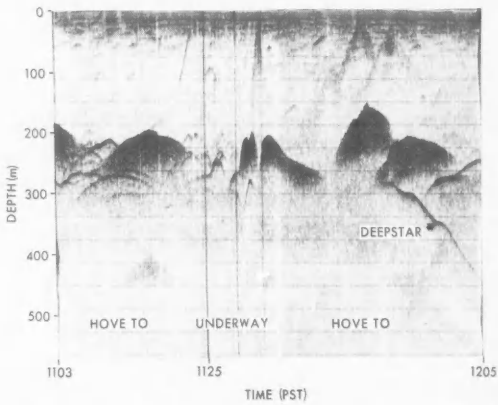

FIGURE 1.—Echogram recorded during *Deepstar* dive 502. The large targets between 150 and 250 m were observed to be schools of anchovy. The discrete traces may have been blue sharks. During the underway portion, the ship was repositioning over the submersible for tracking purposes. The acoustic return from *Deepstar*, a 2-m-diameter sphere, is labeled to provide a qualitative comparison of acoustic reflection strength.

The dive began at 1103 (PST), and a slow descent (13 m/min) was made to 100 m where two blue sharks were observed. This shark is a common species which is easily identified vis-

[1] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

ually. They swam actively out of the gloom, then veered away and circled for a short time before disappearing.

Continuing the descent, at approximately 180 m we became aware of the presence of a large concentration of fish at the periphery of the light field. The descent was stopped and we maneuvered in an attempt to obtain visual and photographic data. Each time the propulsion motors were activated, the fish would hurriedly retreat from view. Their movements were as a disciplined school. Several times we approached the school with the lights out, a technique which enabled the submersible *Alvin* to penetrate schools of myctophids in the Atlantic (Backus et al., 1968). Although we were never able to penetrate the school, the darkened submersible apparently attracted a few individuals who remained near the windows when the lights were switched on. Stunned by the sudden illumination, they remained transfixed long enough for good visual identification. The northern anchovy, with its projecting snout and thin body, is sufficiently distinct from other local clupeoids to give us confidence in our identification. Unfortunately, the photographs taken were blurred.

Three more blue sharks were observed at the same depth as the anchovy school. The deepest sighting was at 275 m. Because these were observed individually, the sightings could all have been of the same individual. Possibly, one of the same sharks sighted at 100 m may have followed *Deepstar* during the descent. We also observed a few squid, presumed to be *Loligo opalescens*, at the depth of the school. The spatial proximity of the sharks, squid, and anchovy suggests a predator-prey relationship, although no predation was observed.

The lower limit of the anchovy school was at 310 m and after dropping below it we descended to 590 m. There we released the descent weight and rose rapidly to the surface. The school was observed between 300 and 200 m during the ascent. The dive ended at 1407.

There is little doubt of the relationship between the anchovies and the large targets on the recording. It is difficult, however, to be sure that there is a correlation between the sharks and the discrete targets. Whatever is responsible for these traces has a high acoustic target strength at 12 kHz. This can be seen by comparison on the figure with the trace made by *Deepstar*, a 2-m-diameter air-filled sphere.

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THE USE OF CONCENTRATION INDICES IN FISHERIES [1, 2]

The temporal-spatial distribution of organisms has generated considerable interest among biologists. This interest has generated many studies which deal primarily with the distribution of a single organism in space. In this note we consider the relationship between two organisms in space or time. We are interested, in particular, in an index of the relation between a predator (a fishing fleet) and a prey (the population to be harvested). We begin by writing

[1] Quantitative Science Paper No. 12. This series is prepared under the general sponsorship of the Quantitative Ecology and Natural Resource Management Program supported by Ford Foundation Grant Number 68-183.

[2] Portions of this study were undertaken while B. J. Rothschild was affiliated with the Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle.

the concentration index, suggested by Gulland (1955), which is the ratio of the ratio of averages catch-per-unit-of-effort statistic to the average of ratios catch-per-unit-of-effort statistic,

$$I_g = \left[\frac{\Sigma c}{\Sigma f}\right] \left[\frac{1}{n}\Sigma \frac{c}{f}\right]^{-1} \qquad (1)$$

where the c denotes catch and the f denotes effort and the summations can extend over either space or time. The index I_g has appeared in many fishery papers such as, for example, Paloheimo and Dickie (1964), Calkins (1963), etc. We can see that when $I_g > 1$, the fishermen tend to be concentrating on the fish, when $I_g < 1$, the fishermen tend to be fishing where the fish are *not* most abundant, and when $I_g = 1$, there is no relation between the distribution of fish and fishermen. It might be mentioned, somewhat parenthetically, that the situation where $I_g < 1$ is rather unusual for single species fisheries, but possible in mixed species fisheries when computed for a single species that is not the main object of the fishery.

Now we observe that when the numerator and denominator of (1) are equal (that is, there is no relation between the distribution of the fish and the fishermen), we can write

$$\frac{\frac{1}{n}\Sigma c}{\frac{1}{n}\Sigma f} - \frac{1}{n}\Sigma \frac{c}{f} = 0 \qquad (2)$$

Now multiply both sides of (2) by $\frac{1}{n}\Sigma f$ and note that whenever we sum a term and multiply by $\frac{1}{n}$ we have the average value of that term which we denote by the operator E, and so (2) becomes

$$E(c) - E\left(\frac{c}{f}\right)E(f) \qquad (3)$$

which is, by definition, the covariance between catch-per-unit-of-effort and effort. It follows then that when the numerator and denominator (the two bracketed terms in (1)) are equal and (2) holds, then (3) must also equal zero, implying that when there is no relation between the distribution of fishermen and fish as indicated by the equality of the numerator and denominator in (1), the covariance between catch-per-unit-of-effort and effort is zero, and hence the correlation between catch-per-unit-of-effort and effort is also zero.

The difficulty with (1) is that it provides an index that is conceptually difficult to interpret, does not contain all of the information that is in the data, is asymmetrical about the point $I_g = 1$, and has no upper bound. All of these difficulties can be alleviated by dividing the covariance in (3) by the geometric mean of the variances of c/f and f, yielding the correlation coefficient,

$$I_r = \frac{\frac{1}{n}\Sigma c - \frac{1}{n}\Sigma \frac{c}{f} \cdot \frac{1}{n}\Sigma f}{\sqrt{\widehat{var}\left(\frac{c}{f}\right) \cdot \widehat{var}\,(f)}} \qquad (4)$$

where $_{var}\,(c/f)$ and $_{var}\,(f)$ refer to the usual sample estimates of variance. Thus I_r will be centered on zero, bounded by —1 and 1. Positive values of I_r imply that high values of effort will be associated with high values of CPUE whereas negative values of I_r imply that high values of effort will be associated with low values of CPUE. When $I_r = 0$, CPUE is not correlated with effort, a condition which, as previously noted, is equivalent to $I_g = 1$.

The fact that I_r contains more information than I_g is demonstrated in the following example based on three contrived sets of data. These data are listed in Table 1 and depicted in Figure 1. We can see that the slopes of lines fitted to each of the three data sets are the same and that I_g for each data set is also the same, but that I_r is different for each data set measuring the variability in c/f for fixed f as well.

In many instances the region in time or space for which these indices are computed will contain relatively few, highly variable, observations. This situation, in particular, raises the question

TABLE 1.—Contrived data under conditions of low, intermediate and high variability which are used to demonstrate the indices I_g and I_r.

Low variability			Intermediate variability			High variability		
c	f	c/f	c	f	c/f	c	f	c/f
10	2	5	6	2	3	2	2	1
10	2	5	14	2	7	18	2	9
49	7	7	35	7	5	21	7	3
49	7	7	63	7	9	77	7	11
Σ 118	18	24	118	18	24	118	18	24
I_g	1.09			1.09			1.09	
I_r	1.00			0.55			0.44	

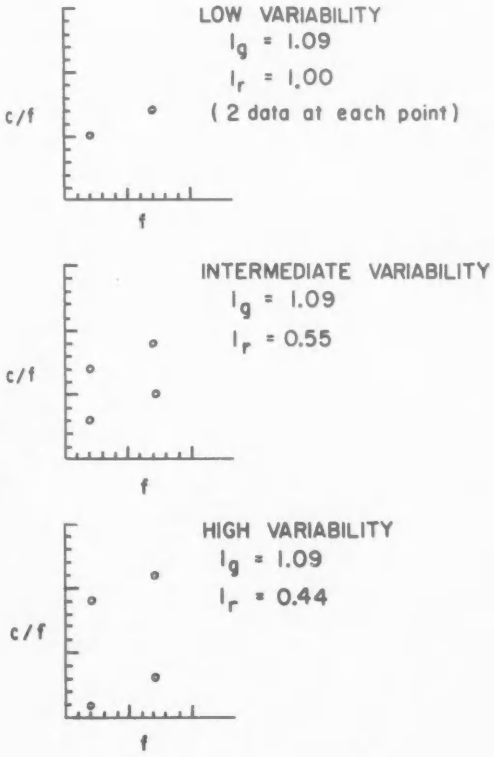

FIGURE 1.—Comparisons of I_g and I_r for c/f and f relations having different amounts of variability. The data are from Table 1.

of the amount of confidence that can be placed in any estimate of I_r or in I_g. The question of confidence can be resolved in the case of I_r if c/f and f are both drawn from the same (at least approximately) bivariate normal distribution. In the likely event that c/f and f are not at least approximately bivariate normal, then perhaps a transformation might be useful. It is also of interest to observe that since I_r is a correlation coefficient then we can interpret I_r^2 as the percentage of the total variability in c/f which is accounted for by regressing c/f upon f. Furthermore there is no reason, of course, why we could not extend this concept in multiple species fisheries to consider these sorts of data in a multiple correlation context.

The idea of using the correlation coefficient measuring the association between c/f and f as a concentration index is intuitively quite obvious and most likely would not be noteworthy except to call attention to the similarity to a commonly used index (I_g) which, in most instances, does not afford as large a scope for interpretation as does I_r. There are some cautions, however, which should be observed and these include, in addition to bivariate normality if we wish to construct confidence intervals, linearity in the relation between c/f and f. If, for example, the gear is saturated or data are pooled from various seasons, then linearity may not be a reasonable underlying model.

In the interpretation of either I_r or I_g it would be helpful to have auxiliary information because without this information it is impossible to determine whether increases in these indices result from an increased concentration of fishing on fish or fish on the location where fishermen happen to be fishing. Thus, these indices alone will not tell us whether changes in apparent abundance result from changes in actual abundance or changes in the skills of fishermen or both.

We should also draw attention to the fact that the relation of c/f and f is generally used in fisheries to determine "optimum" yield by regressing, usually annual, values of c/f upon f. This relation is frequently linear with a negative slope and is usually transformed into a parabolic function of c upon f indicating that level of f for which c is a maximum. The procedure outlined

has been criticized from a statistical point of view because c/f and f are obviously correlated. A measure of the magnitude of this correlation is clearly implied by (3) or (4).

Finally we should point out that our allusion to considering these indices as expressing relation among organisms was not careless because it seems to us that predator-prey relationships might be further elucidated through examination of concentration indices. For example, it would be interesting to relate the catch (in number of prey organisms) per predator stomach to the number of predator stomachs. This, however, is just a special case of the wealth of fishery-fish interaction models which could be applied to the prey-predator situation.

Acknowledgments

We would like to thank D. G. Chapman, Director, Center for Quantitative Science, University of Washington, for reading this note and J. Joseph of the Inter-American Tropical Tuna Commission for stimulating our writing this note.

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SUITABILITY OF INTERNAL TAGS FOR ATLANTIC MENHADEN

Investigations of the Atlantic menhaden resource depend primarily on sampling and analyses of the commercial landings and studies of menhaden biology and ecology. Results of these studies give a broad understanding of the resource but sometimes lack the reliability of more direct evidence. Tagging and recovery of menhaden help provide the reliable information on movements, population size, availability, mortality, and growth rates required to better understand the resource.

The methods by which menhaden are caught, handled, and processed determine some of the requirements for tagging. Menhaden are captured in purse seines and are transferred by suction pumps from the nets to the vessels and from the vessels to the reduction plants. In the plant, the fish are cooked, pressed, dried, and ground into meal. From the time the fish are caught until they are processed into oil and meal, there is little opportunity to handle or see an individual menhaden. Consequently tags or tagged fish must be recovered by mechanical or electronic means. Internal ferromagnetic tags that are mechanically or electronically recoverable have been developed for Atlantic and Pacific herring, Pacific sardine, and anchoveta.

We conducted a series of experiments at Beaufort, N.C., to find a mark suitable for Atlantic menhaden. In 1959 we tagged young menhaden with a nickel-plated, steel tag, (Type A in Figure 1). The tagged menhaden died within a week, terminating the experiment. During 1960 we attempted to mark menhaden with fluorescent pigments and to develop a photoelectric detector. The occurrence of natural fluorescence in menhaden and other marine organisms made discrimination of marked fish impractical (Reintjes, 1963). In 1961-62 we resumed tests with internal tags to select a type suitable for menhaden and to demonstrate its recovery with magnets in a menhaden reduction plant.

Tagging Experiments and Tag Selection

We selected four ferromagnetic tags (Table 1 and Figure 1) for insertion in young Atlantic

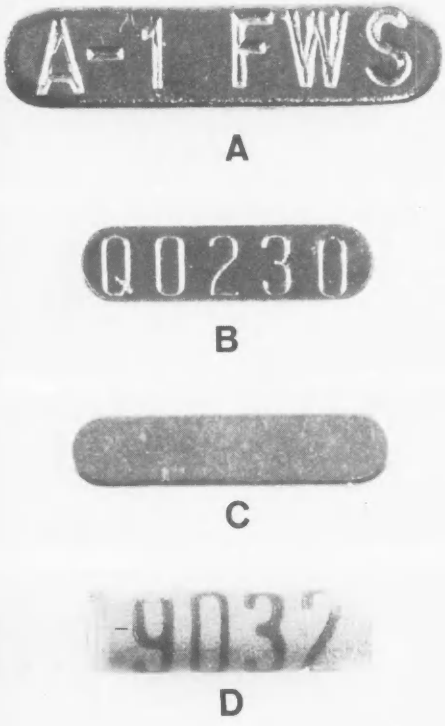

FIGURE 1.—Four ferromagnetic tags tested for marking Atlantic menhaden.

TABLE 1.—Four types of ferromagnetic tags tested for marking Atlantic menhaden.

Type	Materials	Dimensions	Weight	Shape
		mm	g	
A	Nickel-plated steel	19 × 4 × 1.5	0.89	rectangular
B	Nickel-plated steel	12.5 × 3 × 0.6	0.19	rectangular
C	Stainless steel	14 × 2.5 × 0.3	0.15	rectangular
D	Plastic capsule	12 × 3	0.63	cylindrical

menhaden. Type A tags were similar to tags used for Pacific herring (Rounsefell and Dahlgren, 1933) except were twice as thick and had sharp edges. Type B tags, also with sharp edges, were similar to tags used for California sardine (Janssen and Aplin, 1945), anchoveta (Bayliff and Klima, 1962) and anchovy (Vrooman, Paloma, and Jordán, 1966; Haugen, Messersmith, and Wickwire, 1969; Wood and Collins, 1969). Type C tags were similar to tags used for small Atlantic herring in Norway (Dragesund and Hognestad, 1960) and had smooth edges. Type D tags, used for Pacific herring (Wilimovsky, 1963), were dummy radioactive tags that consisted of a gold-plated iron core encased in plastic.

Young menhaden, 115-168 mm fork length, were caught nearby and held in concrete tanks at the laboratory for several weeks prior to the tagging trials. They were fed a homogenized slurry of fish meal and raw hard clams throughout confinement. Test lots of menhaden for each tag type consisted of equal numbers of tagged, incised but not tagged, and handled but not incised or tagged. A fifth lot of fish, not handled, was used as controls.

At tagging, menhaden were transferred to a tank of seawater containing 50 ppm tricaine methanesulfonate (MS-222) until they lost equilibrium. With a scalpel a technician made a small incision on the right side below the midline of the body about midway between the tip of the pectoral fin and the insertion of the pelvic fins to minimize disturbance of viscera. He inserted metal tag Type A, B, or C, into the body with forceps (Figure 2) and Type D through a hollow needle.

The tags and instruments were dipped in a mixture of penicillin G and liquid terramycin. These antibiotics were also added to the anesthetizing tank. All fish were hand-held for 20 sec whether they were tagged, incised, or only handled.

Dead fish and shed tags were removed daily. The dead were measured, weighed, and examined for abnormalities by X-ray and by dissection. The study was concluded in January 1962 when the temperature in the tanks dropped overnight from 3.0° to 0.4°C and most of the fish died. During the preceding 10 weeks the water had cooled gradually from 22°C without killing the fish. Salinity, during this period, ranged from 27 to 32‰.

The Norwegian herring tag, Type C, was the most suitable of the four tested. Tag D was not considered further for it cost ten times more

than the metal tags, and we were not planning to use its radioactive capability.

The numbers of menhaden that died in each tagging experiment are shown in Table 2. Tag Type A caused the most deaths. The combined loss from dying and shedding are shown in Table 3. More menhaden tagged with Types A and B died or shed their tags than did those with Type C. From these trials, Type C was selected for menhaden tagging studies.

Menhaden that died during the experiment and those that survived until the end of the 10-week period were examined for an apparent cause of death. At the end of the 10-week period, all survivors had healed incisions that were faintly visible as slight depressions without scales. Recipients of Type A tags dying during the study had enlarged open wounds and some tags protruded. Types A and B tags found in dead fish or loose on the bottom of the tanks were corroded. The peritoneum did not heal in any incised fish. Muscles were discolored near Types A, B, and D tags, and the tags were imbedded in the mesenteries near the cardiac and pyloric stomachs. Types A and B tags usually were enveloped with tissue. Types C and D tags were better for they apparently caused less irritation.

We were unsuccessful in our attempts to tag smaller menhaden, 75 to 90 mm fork length, in

TABLE 2.—Number of dead Atlantic menhaden in each tagging experiment at the end of 5 biweekly periods. [Number of fish in each lot in parentheses.]

	Number of weeks					
Tag type	2	4	6	8	10	Total
A						
Tagged (86)	1	3	6	2	0	12
Incised only (86)	1	1	0	0	0	2
Handled only (86)	0	1	1	0	0	2
B						
Tagged (86)	2	0	0	0	0	2
Incised only (86)	0	1	0	0	0	1
Handled only (86)	1	2	1	0	0	4
C						
Tagged (86)	1	1	0	0	0	2
Incised only (86)	0	0	0	0	0	0
Handled only (86)	1	1	0	0	0	2
D						
Tagged (33)	0	0	1	0	0	1
Incised only (33)	0	0	0	0	0	0
Handled only (83)	0	1	0	0	0	1
Controls (135)	2	1	0	0	0	3

TABLE 3.—Number of tags lost from experimental groups by death and shedding at the end of 5 biweekly periods. [Number of fish in each group in parentheses.]

	Number of weeks					
Tag type	2	4	6	8	10	Total
A (86)						
Dead	1	3	6	2	0	12
Shed	1	2	2	1	1	7
Total	2	5	8	3	1	19
B (86)						
Dead	2	0	0	0	0	2
Shed	8	2	0	2	2	14
Total	10	2	0	2	2	16
C (86)						
Dead	1	1	0	0	0	2
Shed	0	0	0	0	0	0
Total	1	1	0	0	0	2
D (33)						
Dead	0	0	1	0	0	1
Shed	0	0	0	1	1	2
Total	0	0	1	1	1	3

FIGURE 2.—Inserting a metal tag into the body cavity of young Atlantic menhaden.

August 1962. We used Type C tags but nearly all fish died within 5 days irrespective of treatment. Water temperatures over 30°C were partly responsible for the deaths. No more small menhaden were tagged.

Tag Recovery Trials

We tested the effectiveness of magnets to collect Type C tags in the menhaden reduction plants. Magnets usually are installed in plant conveyor systems to protect the hammermills from stray ferrous metal that breaks off machinery in the plant or is brought in with the fish. Menhaden are cooked and pressed, and the presscake is dried in rotary driers. Most of the dried scrap is pulverized into meal with hammermills.

In the first trial we tagged 102 dead menhaden in the storage or raw box and recovered 60 tags. Nine tags were retrieved from the magnet located after the drier within 8 hr, and the other 51 were collected on a second magnet several days later when the dried scrap was ground into meal (Table 4).

TABLE 4.—Recoveries of 340 tags released in a menhaden reduction plant.

Location and method of release	Number released	Number recovered	Recovery location		Total
			Magnet after drier	Magnet before hammermill	
			%	%	%
Raw box, in fish	102	60	9	50	59
Raw box, in fish	38	26	5	63	68
Cooker input, loose	40	26	12	53	65
Press input, loose	40	35	10	78	88
Press output, loose	40	33	17	65	82
Drier output, loose	40	34	18	67	85
Shed floor, loose	40	34	0	85	85

In the second trial, 238 tags were placed in different locations throughout the plant. Thirty-eight were placed in dead fish in the raw box, and five lots of 40 tags each were scattered loosely in (1) cooker, (2) press input, (3) press output, (4) drier output, and (5) storage shed floor. The recoveries ranged from 65 to 88%. These results showed that recovery of tags was practical with magnets already installed in menhaden plants. We believe the recovery efficiency could be improved by installing additional magnets in the processing system.

We concluded from these preliminary experiments that Atlantic menhaden longer than 115 mm fork length could be tagged internally with a smooth piece of stainless steel and that the tags could be recovered on magnets in the reduction plants.

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FILTRATION EFFICIENCIES OF BOOTHBAY DEPRESSOR TRAWLS

Boothbay Depressor Trawls (Figure 1) are used to obtain yearly estimates of the abundance of larval herring, *Clupea harengus harengus* Linnaeus, in the coastal water of the Gulf of Maine. The Boothbay Depressor trawl is a relatively new device (Graham and Vaughan, 1966), and its use is contemplated by others. It differs from other nets towed for collecting larval fishes in that a large depressor blade is located below the mouth opening and a liner is hung in a larger meshed net some distance from the mouth. These features of construction were examined to determine whether they affected the filtration of water through the trawls. Flow determinations were made about the depressor blade and trawl mouth, and the flow of water through the liner mouth was compared to the ambient flow.

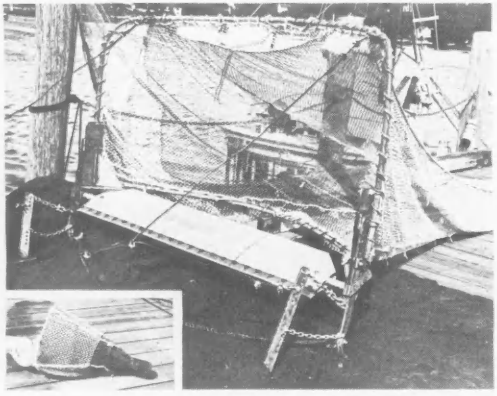

FIGURE 1.—Boothbay Depressor Trawl No. 1. Insert shows wire cod end.

Methods

Nets with a mesh opening of 3.2 cm stretched measure were lashed to pipe frames of 1 × 1.5 m, 1 × 2 m, 1.25 × 3 m, and 1.5 × 4 m (height × width), trawl No. 5, 1, 4, and 2, respectively. These large meshed exterior nets served to hang and protect the small-meshed liners (Table 1) of nylon webbing which retain the larvae. The diameter of the mouth opening for a liner was selected empirically. It was first hung throughout the length of its funnel-shaped exterior net. To reduce friction the liner was progressively shortened toward the cod end until the ratio of wire out to the depth sampled approached 3:1, during repeated tows at 4 to 6 knots. Construction details for the trawls and their respective nets are available from the author.

TABLE 1.—Descriptions of liners used with Boothbay Depressor Trawls.

Trawl type	Total length of liner	Mouth dimension of liner		Mesh diameter	Ratio of open areas
		Height	Width		Mesh/Mouth
	cm	*cm*	*cm*	*mm*	
No. 1	345	53	102	1	7.5
No. 1	579	89	113	2	7.7
No. 1	579	89	113	4	11.2
No. 2	700	152	274	2	5.3
No. 4	510	100	145	2	5.6
No. 5	510	100	145	2	5.6

The filtration efficiency of a No. 1 trawl containing a liner with a mesh opening of 4 mm was determined in a flume (circulating water channel) at the U.S. Navy's David Taylor Model Basin under experimental conditions as described by Mahnken and Jossi (1967). Velocities in the mouths of the pipe frame and the liner were measured by lowering a flow meter at intervals equivalent to its diameter and recording the velocity for each interval with a remote electronic counter. These velocities were then weighted by the area of each interval to obtain an average value for the entire mouth area. Also, a meter was fixed in the center of the forward opening of the wire cod end. Filtration efficiency was measured as the velocity recorded in the net divided by the velocity recorded in the flume; the quotient was expressed as a percentage. Dye was released within the mouths of the net and liner, and tabs were fixed to the blade and nets to trace the direction of the flow of water.

Several tests were made in the field to compare with the results from the flume. Field observations were carried out on (1) the same trawl used in the flume; (2) the trawl No. 2

having the lowest ratio of areas of mesh opening to mouth opening, and thus the lowest potential for efficient straining; and (3) the filtration of the liner mouth opening of trawl No. 5.

Eight flow meters were mounted within the pipe frame and one meter was mounted in the cod end of the same trawl and net (trawl No. 1) used in the flume. The eight meters were distributed peripherally and centrally within the mouth opening of the trawl to sample variations in straining by the net. Upstream and downstream tows were timed over a measured distance within a narrow estuarine channel and the results of the two tows were averaged to adjust for tidal currents. The experiment was repeated using a No. 2 trawl with a liner mesh opening of 2 mm, but flow meters could not be mounted within the liner mouths.

In constructing trawl No. 5, I made the dimensions of the depressor, of exterior net and liner equivalent to the mouth opening of the liner in trawl No. 4. Both the exterior net and the liner extended back from the trawl mouth. Six flow meters were dispersed within the mouth of the liner, one in the cod end, and two were mounted within a small frame outside of the net mouth. In this instance efficiency was considered to be the percentage of the average distance of the upstream and downstream tows recorded by flow meters inside and outside the liner.

I did not weight the velocities recorded in the field according to sectors of the mouth area metered in the net and liner as in the case of flume experiments. In the flume variations in flow were largely vertical, but in the estuary large lateral variations were known to occur. The number of flow meters necessary to make such integrations might have been sufficient to physically affect the flow through the net. A mean velocity recorded by the meters mounted within the mouths of the net and liner was used.

Results and Discussion

The No. 1 trawl was highly efficient at the flume velocities tested. The comparison of the velocities measured in the nets to the flume velocities (Table 2) gave an efficiency of approximately 100%. Efficiency in the cod end approximated 83%. The release of dye and the alignment of tabs showed that the flow of water could be traced horizontally through the net and the liner and that this flow was not diverted by the blade. Moving picture films of the trawl during the test are available from the author.

TABLE 2.—Flume and metered velocities for the Boothbay Depressor Trawl No. 1.

	Net mouth		Liner mouth			Cod end			
	cm/sec		*cm/sec*			*cm/sec*			
Metered velocity	205	309	156	238	314	156	238	309	314
Flume velocity	208	308	156	231	317	126	200	248	262

TABLE 3.—Vessel and metered velocities of the Boothbay Depressor Trawl No. 1 and 2.

	Net mouth	Cod end				
	cm/sec	*cm/sec*				
No. 1 trawl:						
Vessel velocity	184	200	203	192	184	198
Metered velocity	186	187	187	185	188	190
No. 2 trawl:						
Vessel velocity	207	207	222			
Metered velocity	196	157	175			

TABLE 4.—Metered distances of tow for Boothbay Depressor Trawl No. 5.

	Liner mouth		Cod end	
Outside	856	763	854	763
Inside	864	821	601	763

The results from field trials are similar to those obtained in the flume (Tables 3 and 4). Flow efficiencies at the net mouths of the pipe frame and at the liner mouth were comparable to those obtained in the flume. Efficiencies obtained in the cod end of the nets fluctuated around those (80-84%) from the flume. These results suggested that the depressor blade and the hanging of the liner within a larger net did not affect filtration efficiency. The efficiencies were independent of the velocity of towing and the ratio of the mesh to mouth openings, as would be expected with nets that were longer than twice the diameter of their mouth openings (Tranter and Heron, 1967). Further, it is unlikely that the efficiencies would decrease during sampling. Observations in the flume showed that the net and liner would be cleansed constantly during a tow by vigorous peristalsis of

their walls, similarly to that recorded for plankton nets of finer mesh (Tranter and Smith, 1968).

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Fishery Bulletin, Vol. 69, No. 4

LOVE, RICHARD H., "Measurements of fish target strength: A review," p. 703-715.

1) Pages 710 and 711, Figures 4 and 5 were reversed in printing; however, the figure legends are correct.

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